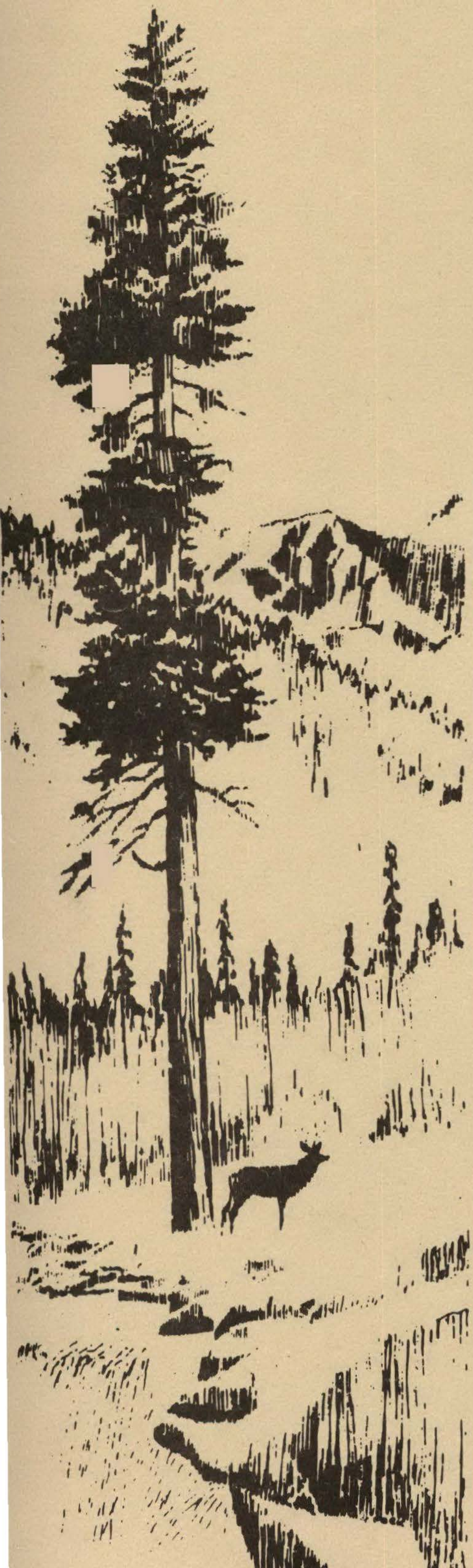
Thesis / Reports
Garton, E.O.

Invesigator/ Study
File



College of Forestry, Wildlife and Range Sciences

IMPACT OF AVIAN PREDATION ON WESTERN SPRUCE BUDWORM

By

Edward O. Garton, John Y. Takekawa,
Lisa A. Langelier, and Mary M. Lawless

November 30, 1984

Forest, Wildlife and Range Experiment Station

University
of Idaho

Final Report under Cooperative Agreement PNW-83-302

to

CANUSA Spruce Budworms Program West
USDA Forest Service
Pacific Northwest Forest and Range Experiment Station
Portland, Oregon

IMPACT OF AVIAN PREDATION ON WESTERN SPRUCE BUDWORM

By

Edward O. Garton, John Y. Takekawa,
Lisa A. Langelier, and Mary M. Lawless

November 30, 1984

Fish and Wildlife Department, University of Idaho

Moscow, Idaho 83843

TABLE OF CONTENTS

Preface i

Section One:

Functional response of avian predators of the western spruce budworm 1

Section Two:

How much is an evening grosbeak worth? 42

Section Three:

Biological control of forest insect outbreaks: The use of avian predators 57

Section Four:

Habitat requirements of avian predators 71

Section Five:

Effects of stand characteristics on avian predators of western spruce budworm 79

PREFACE

This final report completes work under Cooperative Agreement PNW-83-302. It includes the results of work not described in previous reports. These other reports should also be consulted for a fuller understanding of the impact of avian predation on western spruce budworm populations:

Garton, E. O., L. A. Langelier, M. M. Lawless and J. Y. Takekawa. Management of avian predation on western spruce budworm. Final report submitted November 4, 1983. 120p.

Garton, E. O., P. T. Sullivan, J. Y. Takekawa, L. A. Langelier and M. M. Lawless. Stomach contents of avian predators of western spruce budworm. Final report submitted November 4, 1983. 10p.

Some of this material has been published (Section 2 and Section 3) and may be cited freely. The remaining parts are in press or in preparation and may not be cited without written permission of the authors.

SECTION CNE

Functional Response

FUNCTIONAL RESPONSE OF AVIAN PREDATORS OF THE WESTERN SPRUCE BUDWORM

John Y. Takakawa and Edward O. Garton

Abstract: Passerine birds may contribute significantly to regulation of the western spruce budworm. The functional responses of four abundant western forest birds were examined in laboratory foraging trials at low budworm densities. The evening grosbeak, pine siskin, and western tanager responded strongly to increases in the density of the budworm, but the chipping sparrow did not vary its consumption. The two flocking species, the evening grosbeak and pine siskin responded most strongly to increases in the budworm population at low density levels. They also consumed the most budworm. Holling's functional response equation was used to model the response and predict maximum consumption rates. Potential maximum consumption ranged from 8 budworm/hour for the chipping sparrow to 214 budworm/hour for the evening grosbeak. Consumption predicted from laboratory foraging trials was compared to stomach contents data to estimate a range within which actual consumption occurs. Each species was found to prefer larger larval instars in cafeteria trials and in foraging

bouts. Managing for avian predators which exhibit strong functional responses may contribute most to stabilizing the population of an insect at low densities and prevent outbreaks.

Passerine birds are beneficial predators of many insect pests (Poznanin 1956, Bruns 1960, Franz 1961, Herberg 1965, Buckner 1966, Buckner 1970, Otvos 1979, Takekawa _et al._ 1982). Birds decrease survival of insect populations in a density-dependent manner if they consume proportionately more insects as the population increases in abundance (Hagen _et al._ 1971). Avian predators may respond in two ways to increases in the density of their prey: functionally and numerically (Solomon 1949).

A species responds functionally when the individual predators increase their consumption of an insect when the density of that insect increases (Solomon 1949). A species responds numerically if the number of birds increases with increasing prey density. The numerical response may be immediate through migration of birds to an outbreak area, or delayed following increased reproduction of young or higher fledgling survival (Solomon 1964). The product of the functional and numerical responses is the total response of an avian predator to changes in the density of its prey.

Birds may play a very important role as regulators of forest insect populations at endemic to low epidemic densities (Thomas et al. 1975, Wiens 1975). Birds often increase dramatically in numbers during outbreaks of pest insects and may contribute substantially to control these outbreaks (Blais and Parks 1964). Species which respond functionally at low densities may actually prevent outbreaks by stabilizing population fluctuations. This role has not been quantified because it is difficult to census changes in low density populations of insects with reasonable precision.

Our studies of avian predators of the western spruce budworm (Choristoneura occidentalis) are part of a joint Canadian and U.S. Forest Service research project (CANUSA) investigating the biology, population dynamics, and management of this important forest insect pest. Budworm larvae defoliate economically valuable trees such as Douglas-fir (Pseudotsuga menziesii), true fir (Abies spp.), and spruce (Picea spp.). Damage caused by the budworm is usually limited to decreased growth or vigor of attacked trees, but defoliation may be extensive enough to cause tree mortality through topkill (U.S. Forest Service 1976).

In this paper, we examine the functional response of four avian predators of the budworm at low budworm densities in laboratory trials. The chipping sparrow (Spizella passerina), evening grosbeak (Hesperiphona vespertina), pine siskin (Pinus spinus), and western tanager (Piranga *ludoviciana*) are four major budworm predators representative of three different foraging guilds. These species are ubiquitous and abundant members of forest communities throughout the west and are efficient budworm consumers (E.O. Garton, unpublished data).

METHODS

Species selected for laboratory study were mistnetted in budworm outbreak areas of north-central Washington. They were transported to an experimental aviary at the University of Idaho. The birds were held in small holding pens connected to a large observation room where trials were conducted. Six chipping sparrows, 12 evening grosbeaks, 5 pine siskins, and 11 western tanagers were tested over a two-year period.

Two 6-foot tall "trees" made of lumber were constructed to support 6 Douglas-fir branches, 3 branches on each tree. Budworm larvae were obtained from the U.S. Forest Service Forest Entomology Laboratory at Berkeley, California, or they were reared from nondiapausing hibernacula supplied by the Forest Sciences Laboratory in Corvallis, Oregon. Budworm were measured and placed on the branches and their location was recorded. Budworm were planted on the branches on small pieces of flypaper attached to buds because new foliage was not available for the insects to spin into. Individual birds and different budworm arrangements used for the trials were chosen in a random order. Ten low density levels of 1,2,3,4,5,6,9,12,15, and 18 budworm on six branches were selected for the trials. Each density was replicated 5 times using 5 different individuals. Observers standing behind a one-way window used a digital data recorder (datalogger) to make a continuous behavior record for each trial. The datalogger was used to record nonforaging time, the duration of foraging maneuvers, and the time it took to capture and handle prey. The trials were limited to 8 minutes to prevent satiation.

The number of trials for each species varied over the two-year study period because of the difficulty in obtaining budworm and keeping them alive. Chipping sparrows were tested 105 times, evening grosbeaks 129, pine siskins 96, and western tanagers 141. Consumption was adjusted to budworm taken per hour of foraging time by subtracting time the birds spent obviously nonforaging. Densities were reported in budworm per square meter of foliage which is the most commonly used measure in field studies. A series of analysis of variance (AOV) tests for unbalanced sample designs were applied to the data to examine the functional response of the different species (SAS Institute 1979).

Cafeteria feeding trials were conducted to test for differences in preference between 3rd, 4th, 5th, and 6th instar larvae and pupae. Birds were presented with three stages at one time because during budworm development no more than three stages are seen at once. Selection for larval stages was also examined during foraging trials. Preference was calculated as the number consumed divided by the number expected to be taken when equal proportions of each stage was presented. Differences between stages selected were tested with a chi-square statistic (Zar 1974) and significant preferences were identified (Neu et al. 1974).

RESULTS

A 2-way AOV test was used to test the null hypothesis that there was no difference in the number of budworm consumed by the different species across four budworm density levels (<1.5, 1.5-3.0, 3.0-4.5, >4.5 budworm /m^2). The null hypothesis was rejected ($p<.0001$) for the species-density interaction term indicating that functional responses differed between the different species.

Each species was then tested by a one-way AOV test to see which had a significant response to changes in budworm density during the trials (Table 1). The evening grosbeak ($p<.0001$), pine siskin ($p=.0001$), and western tanager ($p=.0073$) showed significant functional responses. The chipping sparrow ($p=.6274$) did not have a significant

Table 1. Functional response of chipping sparrow, evening grosbeak, pine siskin, and western tanager based on laboratory foraging trials. Budworm numbers consumed at different densities by one species were compared with a one-way AOV test for unbalanced designs, and significant differences were located with a least squares difference test (SAS Institute 1979).

	Chipping Sparrow		Evening grosbeak		Pine siskin		Western tanager	
Density	Mean	Grouping*	Mean	Grouping*	Mean	Grouping*	Mean	Grouping*
<1.5	8.1	A	8.8	A	15.3	A	9.5	A
1.5-3.0	8.5	A	24.2	B	19.1	A B	18.4	A B
3.0-4.5	2.3	A	37.9	C	29.9	B	29.8	C
≥ 4.5	7.9	A	49.0	C	44.9	C	24.4	C B
F-statistic	F = 0.59		F = 27.20		F = 14.34		F = 4.20	
Probability level	p = .6274		p = .0001		p = .0001		p = .0073	

* Different letters indicate significant differences in budworm consumed when a least squares difference test is applied (SAS Institute 1979).

response but consumed an average of 8.04 budworm per hour (SE=1.321) over the range of trial densities.

The species were compared at four density levels (<1.5, 1.5-3.0, 3.0-4.5, >4.5 budworm/m²) to see where the birds differed in their functional response. At three density levels there was a significant difference in the number consumed by at least two of the species (Table 2). A least-squares difference test was applied to locate the differences (SAS Institute 1979). At low density (<1.5 budworm/m²) the pine siskin consumed more budworm than the other 3 species, but not significantly so. From densities of 1.5-3.0 and 3.0-4.5 budworm/m², the chipping sparrow took significantly less than the other 3 species. Finally, at higher densities (>4.5 budworm/m²), the two flocking species took more than the tanager, which in turn consumed more than the sparrow.

Modeling the Response

Several models have been proposed to describe functional response (Lotka 1925, Volterra 1926, Gause 1934, Nicholson and Bailey 1935, Holling 1959, Watt 1959, Murton *et al.* 1963, Goss-Custard and Bothery 1976). The Holling model (1959) was chosen to describe the functional response of avian predators of budworm because it has been shown to

Table 2. Mean budworm consumed per hour at low density by chipping sparrow, evening grosbeak, pine siskin, and western tanager based on laboratory foraging trials. The budworm taken by each species was compared at each density with a one-way AOV test for unbalanced designs, and a least-squares means test was applied to locate significant differences (SAS Institute 1979).

Budworm Density (Larvae/m^2 foliage)

< 1.5			1.5-3.0			3.0-4.5			≥ 4.5		
Species	Budworm Taken*	n	Species	Budworm Taken*	n	Species	Budworm Taken*	n	Species	Budworm Taken*	n
Pine siskin	15.3 A	35	Evening grosbeak	24.2 A	42	Evening grosbeak	37.9 A	11	Evening grosbeak	49.0 A	45
Western tanager	9.5 A	26	Pine siskin	19.1 A	21	Pine siskin	29.9 A	10	Pine siskin	44.9 A	29
Evening grosbeak	8.8 A	30	Western tanager	18.4 A	27	Western tanager	29.8 A	26	Western tanager	24.4 B	60
Chipping sparrow	8.1 A	34	Chipping sparrow	8.5 B	40	Chipping sparrow	2.3 B	10	Chipping sparrow	7.9 C	20
F-statistic	F = 5.11		F-statistic	F = 5.47		F-statistic	F = 4.35		F-statistic	F = 18.67	
Probability level	p =.0024		Probability level	p =.0016		Probability level	p =.0083		Probability level	p =.0001	

* Different letters indicate significant differences in budworm consumed when a least squares difference test is applied (SAS Institute 1979).

fit real data well in many predator-prey systems (Holling 1959, Griffiths 1969, Ware 1972, Hardman and Turnbull 1974).

Holling's functional response model is based on four assumptions;

1) The predator searches for one prey
2) The predator spends all of its time foraging
3) Search rate and handling time are constant (unaffected by satiation, learning)
4) Searching and handling times are exclusive

The model is of the form:

$$N = aXT(s) \tag{1}$$

where N= prey consumed, a= rate of search (a constant), X= density of the prey, and T(s)= search time. Holling separated the foraging time (T) into a handling time T(h) and a search time T(s).

$$T = T(s) + T(h) \tag{2}$$

Assuming that handling time per prey (h) is constant,

$$T(h) = hN$$

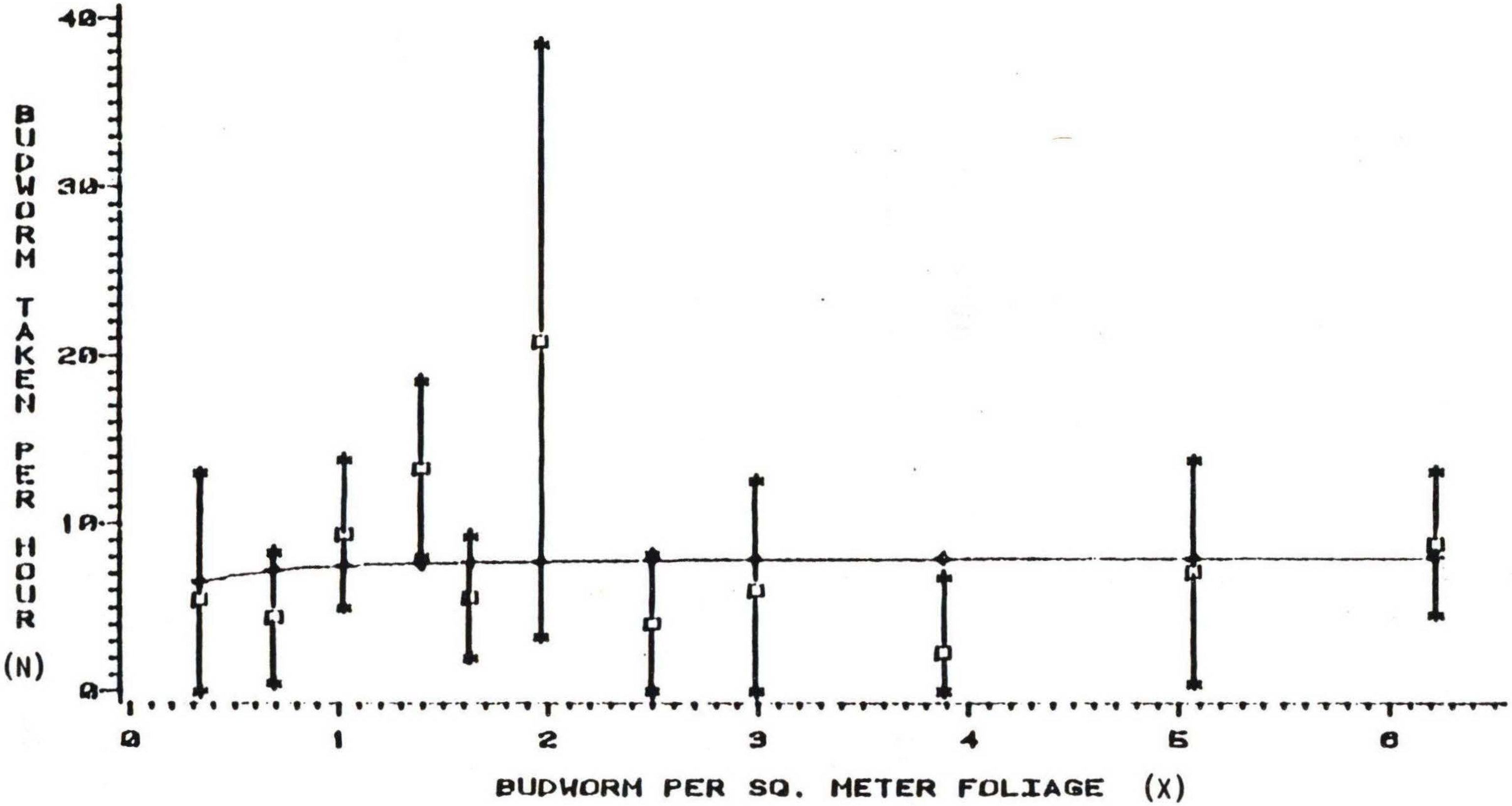
and,

$$T(s) = T - hN \tag{3}$$

Substituting (3) into (1) and solving for N:

$$N = \frac{aTX}{1+ahX} \tag{4}$$

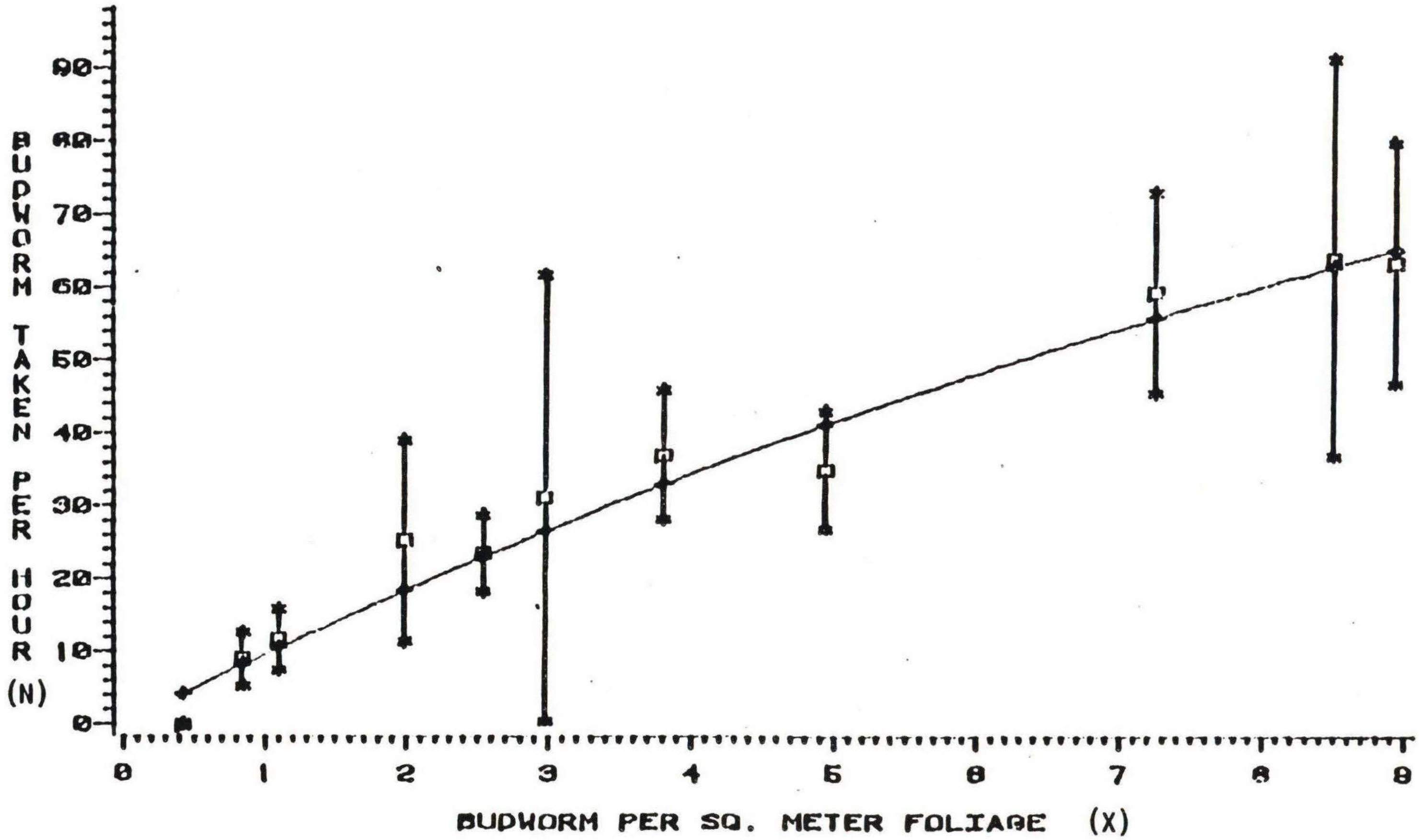
Holling's model was fit to data from laboratory trials using least-squares nonlinear regression (Marquardt 1963: Figure 1-4), and estimates of model parameters of handling time (h) and search rate (a) were obtained for each species



□ Mean budworm consumed (95% confidence interval)

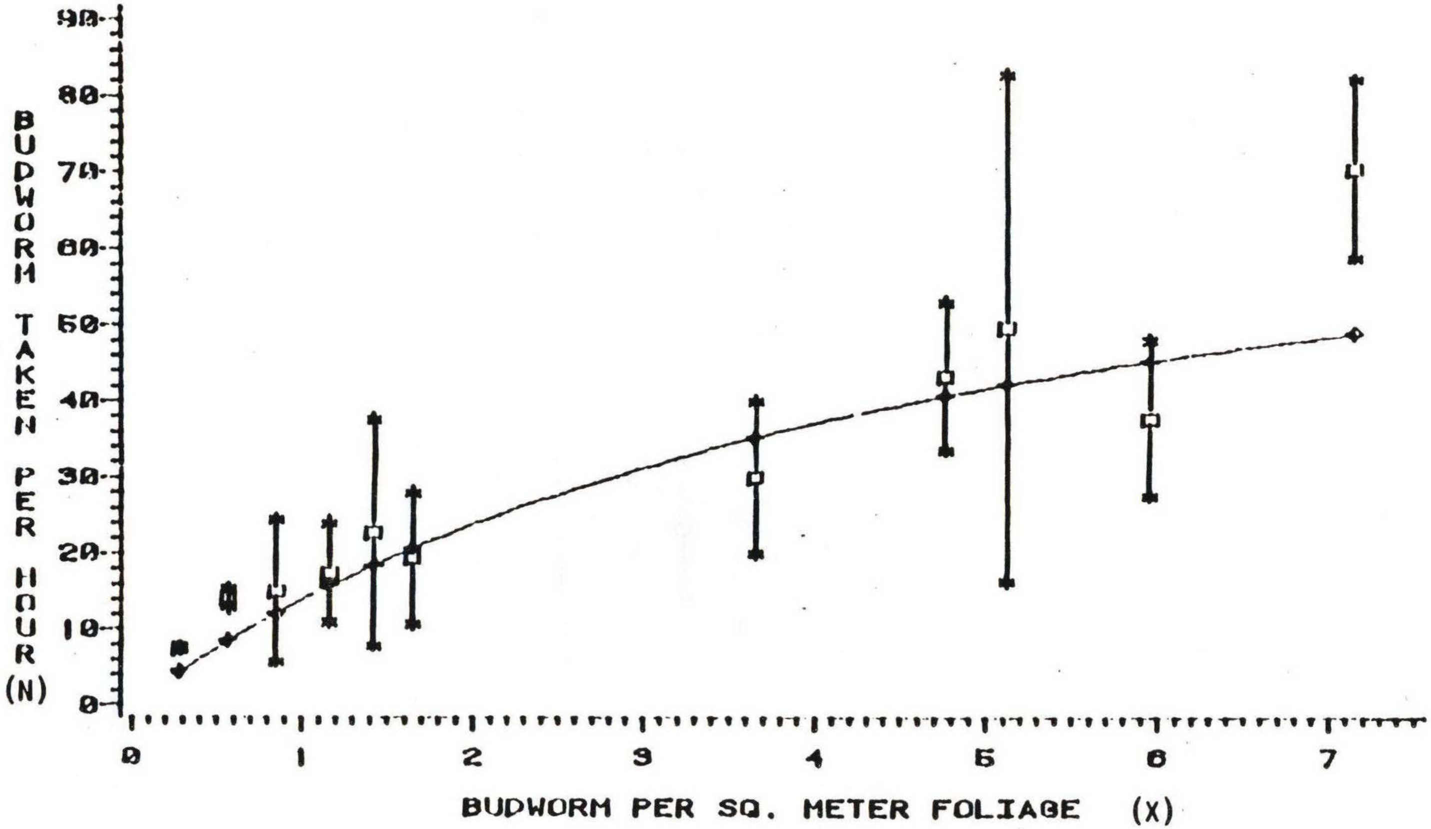
◇ Predicted consumption

Figure 1. Functional response of chipping sparrow fitted with the Holling model: $N = aTX / (1 + ahX)$.



□ Mean budworm consumed (95% confidence interval)
◇ Predicted consumption

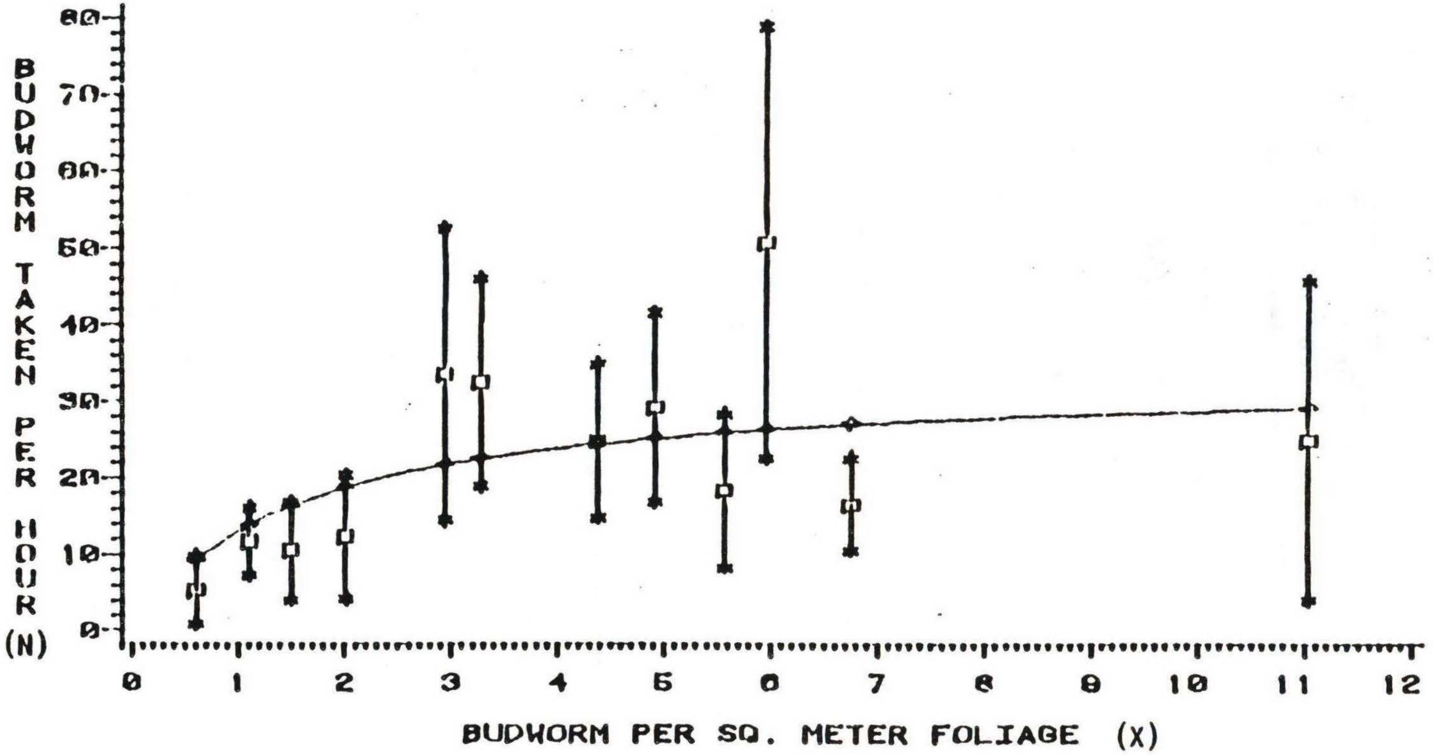
Figure 2. Functional response of evening grosbeak fitted with the Holling model: $N = aTX / (1 + ahX)$.



□ Mean budworm consumed (95% confidence interval)

◇ Predicted consumption

Figure 3. Functional response of pine siskin fitted with the Holling model: $N = aTX / (1 + ahX)$.



□ Mean budworm consumed (95% confidence interval)
◇ Predicted consumption

Figure 4. Functional response of western tanager fitted with the Holling model: $N = aTX / (1 + ahX)$.

Table 3. Functional response of four avian predators based on laboratory foraging trials. Parameters for the Holling model, N = aTX / (1+ahX) were estimated by least squares nonlinear regression (Marquardt 1963).

SPECIES	n	Parameter Estimates (SE) Handling time (h)	Search rate (a)
Chipping sparrow	105	.124 (.0337)	104.1 (458.60)
Evening grosbeak	129	.004 (.0024)	10.0 (1.51)
Pine siskin	97	.012 (.0038)	16.7 (4.41)
Western tanager	141	.030 (.0067)	21.3 (11.23)

(Table 3).

Handling times predicted by the model for each species were found to differ significantly from handling times observed and recorded during the trials (Table 4). The model predicted a larger handling time for all species which implies at least one assumption of the model was not met. The laboratory trials were conducted with one prey and only foraging time was included in the analysis.

Potential maximum consumption for each species is estimated as the total budworm consumed assuming that budworm are so abundant that no time is spent searching. The reciprocal of the handling time may be used to estimate maximum consumption (Table 5). The density of budworm at the predicted maximum consumption point cannot be calculated directly since the model is asymptotic. However, at an arbitrary fraction of 90 percent of the maximum, the density can be calculated as:

$$X = \frac{N}{aT - Nah} \tag{5}$$

The estimated density near the asymptotic maximum consumption value differs greatly between species (Table 5).

Functional response may also be estimated from analysis of digestive tracts of birds collected in the field (E.O. Garton, unpublished data). The number of budworm per stomach was divided by the digestive passage rate estimated from field trials to convert consumption to budworm per hour (Table 8). The grosbeak, siskin, and tanager all had

Table 4. Observed handling times recorded during foraging trials compared to predicted handling times estimated by the Holling model. A t-statistic of the form, t = Observed-Predicted/ Standard Error (Observed) was used to test if the observed and predicted values were significantly different.

		Handling time (hr)		Test of Significance	
SPECIES	n	Observed (SE)	Predicted	t-statistic	Probability level
Chipping sparrow	69	.012(.0016)	.124	69.26	$p < .001$
Evening grosbeak	120	.003(.0003)	.004	3.94	$p < .001$
Pine siskin	282	.007(.0003)	.012	18.09	$p < .001$
Western tanager	179	.007(.0004)	.030	62.30	$p < .001$

Table 5. Potential maximum consumption by four budworm predators and the predicted density at which 90% of maximum consumption would be reached. Maximum consumption was predicted as the number consumed assuming all foraging time was spent handling prey (1/handling time). Budworm densities at 90% of maximum consumption were calculated from the equation X = N/(aT-Nah).

SPECIES	Predicted Maximum Consumption (budworm/hr)	Budworm Density at 90% maximum consumption (budworm/m^2)
Chipping sparrow	8.0	0.7
Evening grosbeak	213.8	212.7
Pine siskin	83.0	44.8
Western tanager	33.3	14.1

Table 6. Handling times and search rates predicted by the Holling model based on laboratory foraging trials and stomach analyses.

SPECIES	Laboratory Foraging Trials Parameter Estimates (hr)		Collection Data Parameter Estimates (hr)	
	Handling time	Search rate	Handling time	Search rate
Chipping sparrow	.1244	104.17	.1185	28.83
Evening grosbeak	.0042	10.05	.0346	235.35
Pine siskin	.0121	16.69	.0486	31.45
Western tanager	.0300	21.28	.6059	4.83

responses which were higher in laboratory trials than were shown from collection data (Figure 5-7). The chipping sparrow, with very little response, showed almost no difference foraging in laboratory trials and in the field (Figure 8).

Preference

Laboratory trials were conducted in a single prey environment since the objective was to identify the efficiency of the predators feeding on budworm. During feeding box trials conducted in the field, birds placed in 4x4x4 foot cages showed a strong preference for budworm when other arthropods were present (Garton 1980). When budworm larvae are available, they are probably preferred by many bird species because they are soft-bodied insects that are easily captured. They are also highly obvious to most birds that forage in conifers (Morris *et al.* 1958).

Initially, the budworm that were obtained were of three different color strains: green, calico, and dark. Initial trials on evening grosbeaks presented with these strains showed that one strain was not preferred above another (X^2= 1.9056,.50<p<.25). Thus, the rest of the trials were conducted with mixed budworm.

Cafeteria trial results for the four species indicated

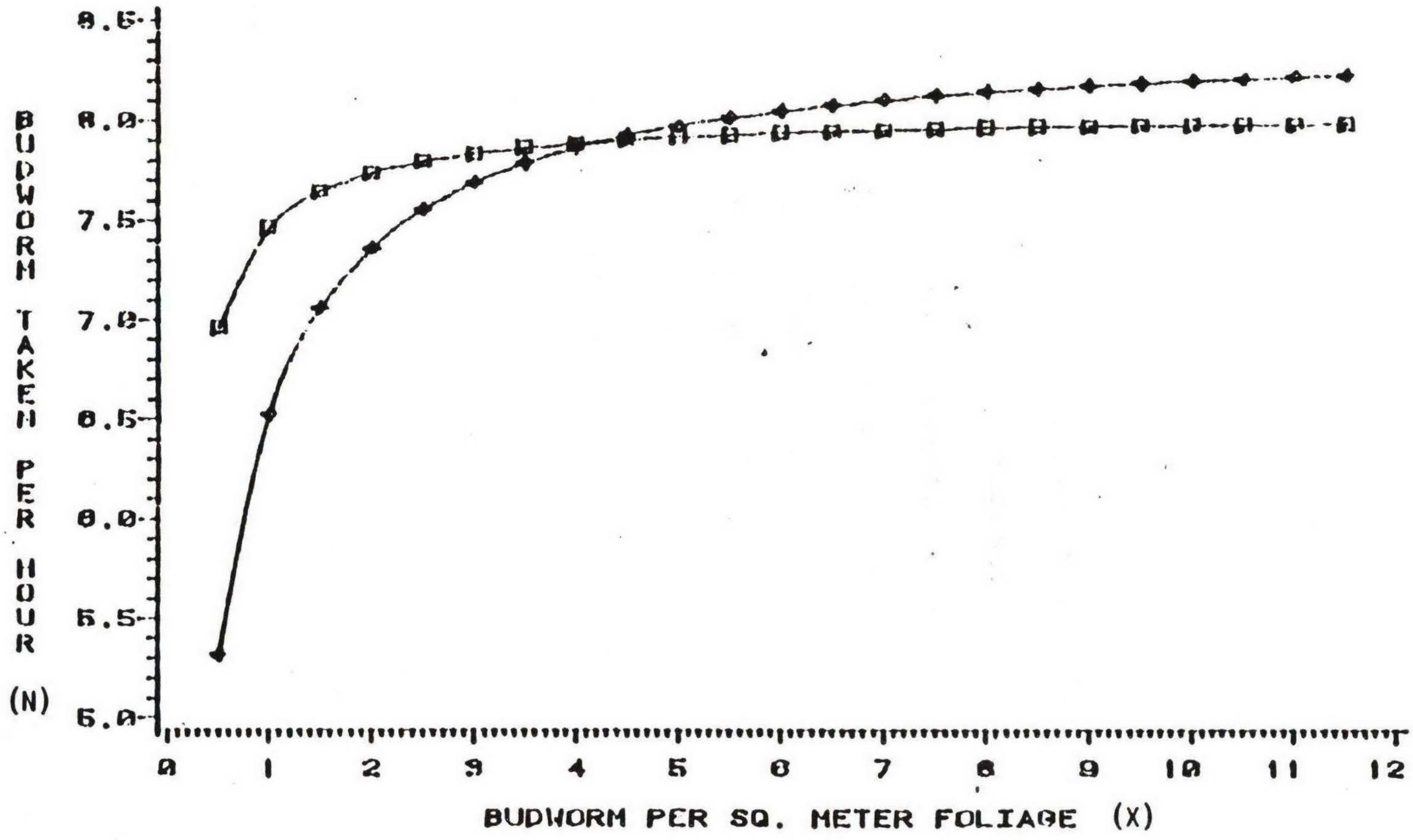


Figure 5. Functional response of chipping sparrow based on laboratory foraging trials (□) and collection data (◇).

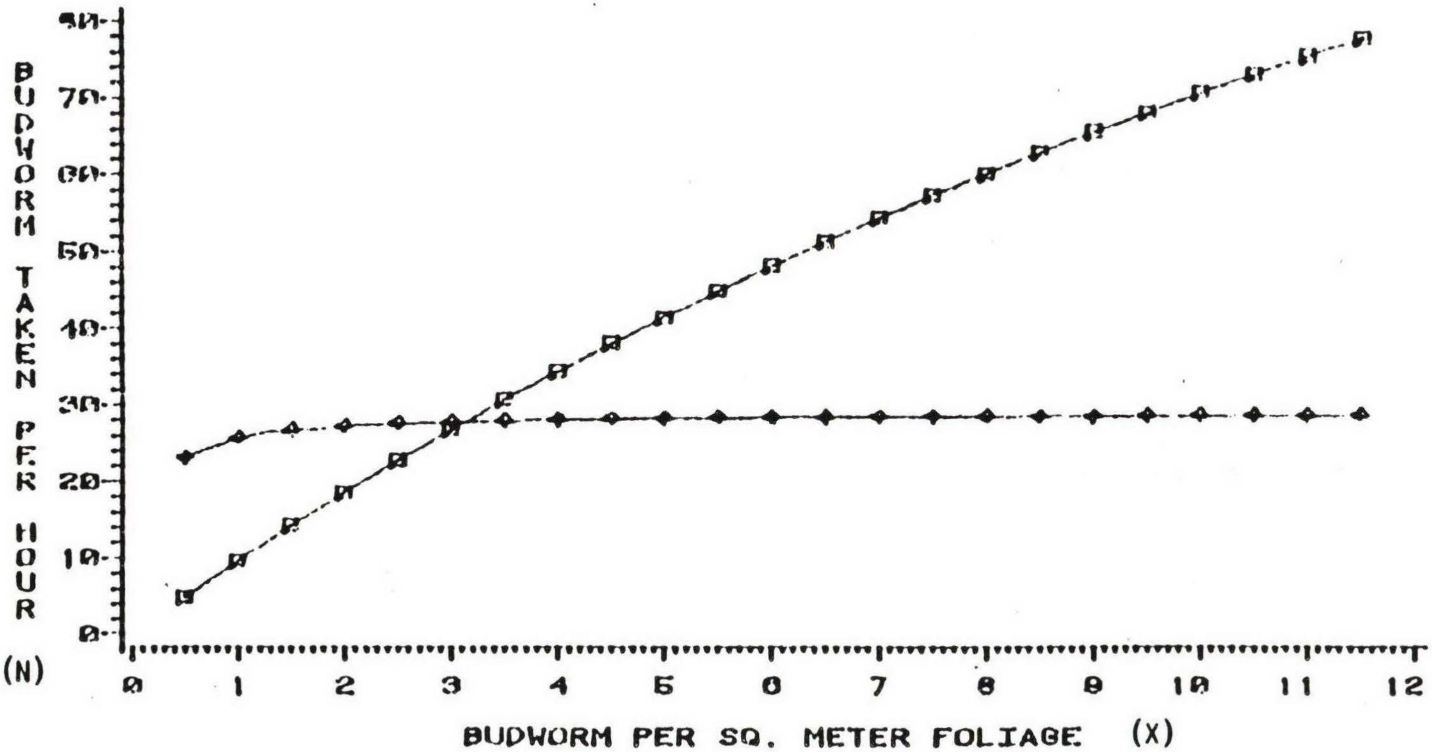


Figure 6. Functional response of evening grosbeak based on laboratory foraging trials (□) and collection data (◇).

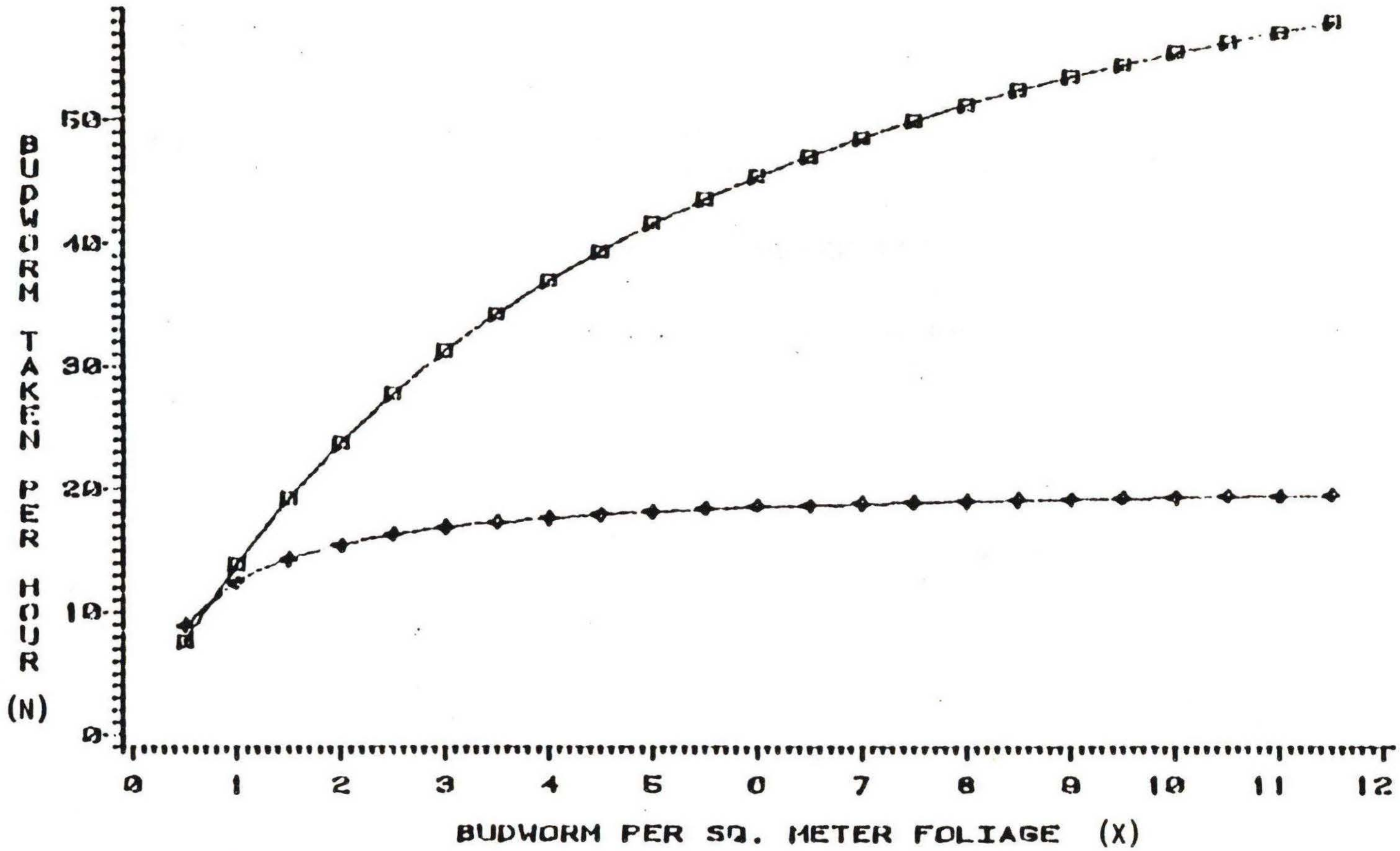


Figure 7. Functional response of pine siskin based on laboratory foraging trials (□) and collection data (◇).

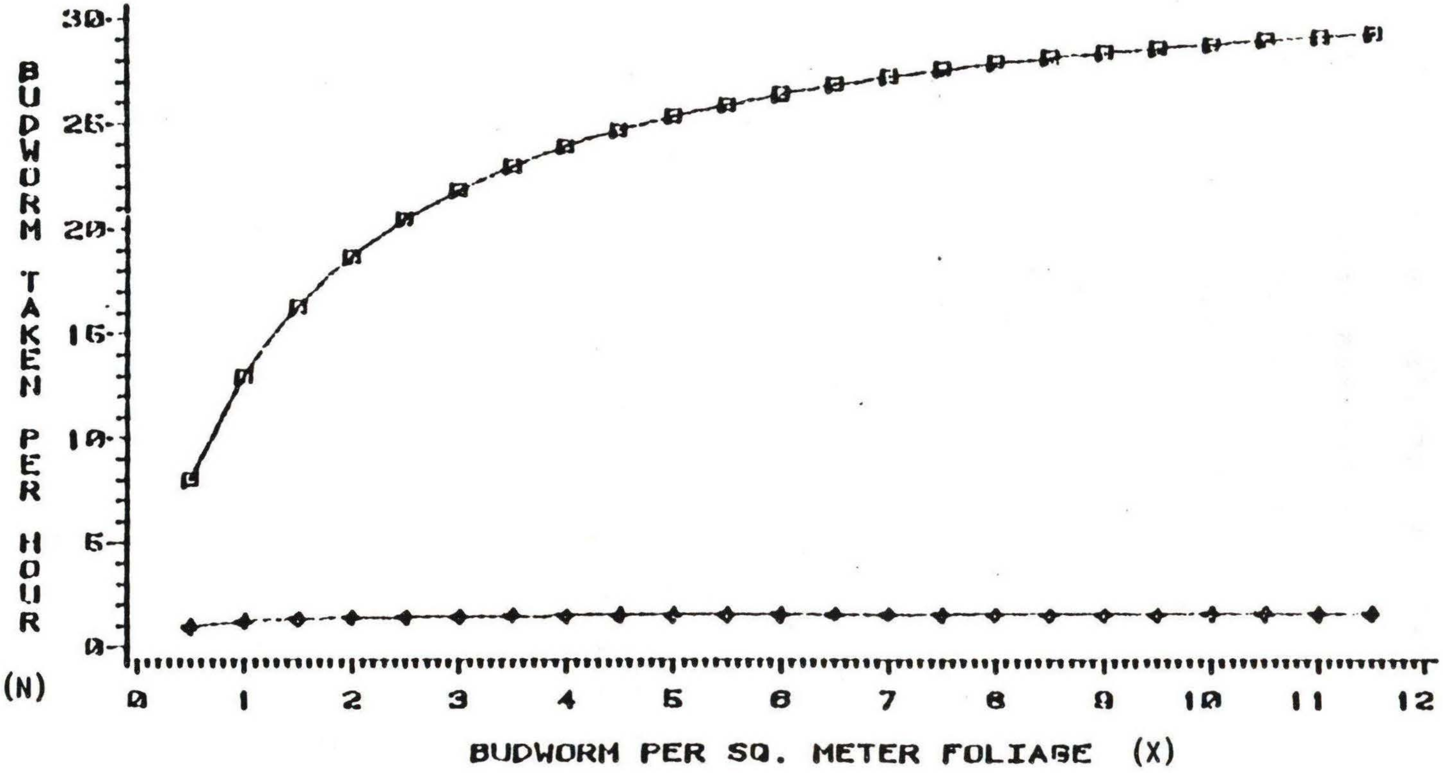


Figure 8. Functional response of western tanager based on laboratory foraging trials (◻) and collection data (◇).

that larger larval stages were preferred by all species with the exception of the small-billed pine siskin which preferred 5th instar larvae over 6th (Table 7). Pupae were avoided by grosbeaks and chipping sparrows but were preferred by tanagers and siskins.

During laboratory foraging trials, sizes of budworm were recorded to see if a preference was expressed when the birds were actively foraging. Nearly all of the trials were conducted with 5th and 6th instar larvae. All species preferred 6th instar larvae over 5th although preference by the chipping sparrow was nonsignificant (Table 8). There was no difference in preference for larger budworm between predator species despite differences in body size and foraging behavior.

DISCUSSION

There are 640 species of breeding birds in North America; 283 forage in forested areas and consume insects in 10 percent or more of their diet (Jackson 1979). Biological control of economically important insects may be possible by increasing the density of insect-consuming birds in areas susceptible to insect outbreak. Control with birds would be most effective if species or guilds which exhibit strong functional responses at low insect densities were

Table 7. Preference for larval instars and pupae of western spruce budworm in cafeteria feeding trials. Preference ratios were calculated by dividing the number of budworm consumed by the number expected to be taken given equal availability of each stage. Differences were tested with a chi-square statistic (Zar 1974).

		Preference Ratio							
		Larval Instar						χ^2	
Trial	SPECIES	3	4	5	6	Pupae	n	statistic	Significance level
1	Chipping sparrow	0.20*	1.50	1.30			30	9.80	$.005 < p < .01$
	Evening grosbeak	0.23*	1.13	1.65*			40	13.88	$p < .001$
	Pine siskin	0.40*	0.70	1.90*			30	12.60	$.001 < p < .005$
	Western tanager	0.66	0.51	1.83*			59	20.58	$p < .001$
2	Chipping sparrow		0.50	0.80	1.70*		30	7.80	$.05 < p < .10$
	Evening grosbeak		0.20*	1.00	1.80*		45	19.20	$p < .001$
	Pine siskin		0.40*	1.50	1.10		30	6.20	$.025 < p < .05$
	Western tanager		0.41*	0.89	1.70*		44	12.59	$.005 < p < .001$
3	Chipping sparrow			0.50	2.00*	0.50	30	15.00	$p < .001$
	Evening grosbeak			0.98	1.28	0.75	40	1.85	$p < .20$
	Pine siskin			0.70	0.70	1.60	30	5.40	$.05 < p < .10$
	Western tanager			0.89	0.75	1.36	44	3.04	$.03 < p < .02$

*A preference ratio (P.R.) significantly different from 1.0 ($p \leq .01$) indicating preference for (P.R. > 1.0) or avoidance of (P.R. < 1.0) a budworm stage (Neu *et al.* 1974).

Table 8. Preference for larval instars of western spruce budworm in laboratory foraging trials. Preference ratios were calculated by dividing the number consumed by the number expected to be taken if each stage was taken in proportion to its availability. Differences were tested with a heterogeneity chi-square test (Zar 1974).

	Number Consumed (Expected) Larval Instar Stage					
SPECIES	5	6	n	χ^2	Degrees of Freedom	Significance level
Chipping sparrow	13 (14.83)	18 (16.27)	31	.43	1	$.50 < p < .75$
Preference ratio	.88	1.11				
Evening grosbeak	119 (143.32)	179 (154.67)	298	7.95	1	$.001 < p < .005$
Preference ratio	.83	1.16				
Pine siskin	81 (102.10)	158 (136.91)	239	7.61	1	$.005 < p < .01$
Preference ratio	.79	1.15				
Western tanager	126 (151.29)	185 (159.71)	311	8.23	1	$.001 < p < .005$
Preference ratio	.83	1.16				
TOTAL χ^2				24.23	4	$p < .001$
Pooled χ^2	339 (411.54)	540 (467.45)		24.08	1	$p < .001$
Preference Ratio	.82	1.16				
Heterogeneity χ^2						$.975 < p < .99$

encouraged. Species which consume a greater proportion of an insect population as it increases would contribute to stability of the population (Oaten and Murdoch 1975).

All three of the foliage-gleaning species we examined in laboratory trials had a strong functional response to the budworm (Figure 9). The ground-foraging chipping sparrow did not show a discernible functional response. It may be poorly adapted for foliage-gleaning even when there is an abundance of prey. Simmons (1968) found that jack pine budworm (_C. pinus_) emitted a gut secretion that repulsed chipping sparrows. The western spruce budworm also secretes a gut fluid, and the secretion may have a similar effect.

Surprisingly, the omnivorous flocking birds, the evening grosbeak and the pine siskin, had responses significantly greater than the insectivorous western tanager. The flocking species proved to be extremely efficient budworm consumers despite their morphological adaptation for seed consumption (Bent 1943, Martin _et al._ 1951). Their specialized conical bills may be a product of selection during times of stress such as winter periods when seeds are available but insects are scarce. These birds commonly feed on seeds and buds (Martin _et al._ 1951) and may be the best adapted species for foraging on the tips of branches where defoliating larval insects are found.

The pine siskin consumes the most budworm at very low density levels (< 1.5 budworm/m^2), but it consumes virtually the same amount as the evening grosbeak at higher endemic

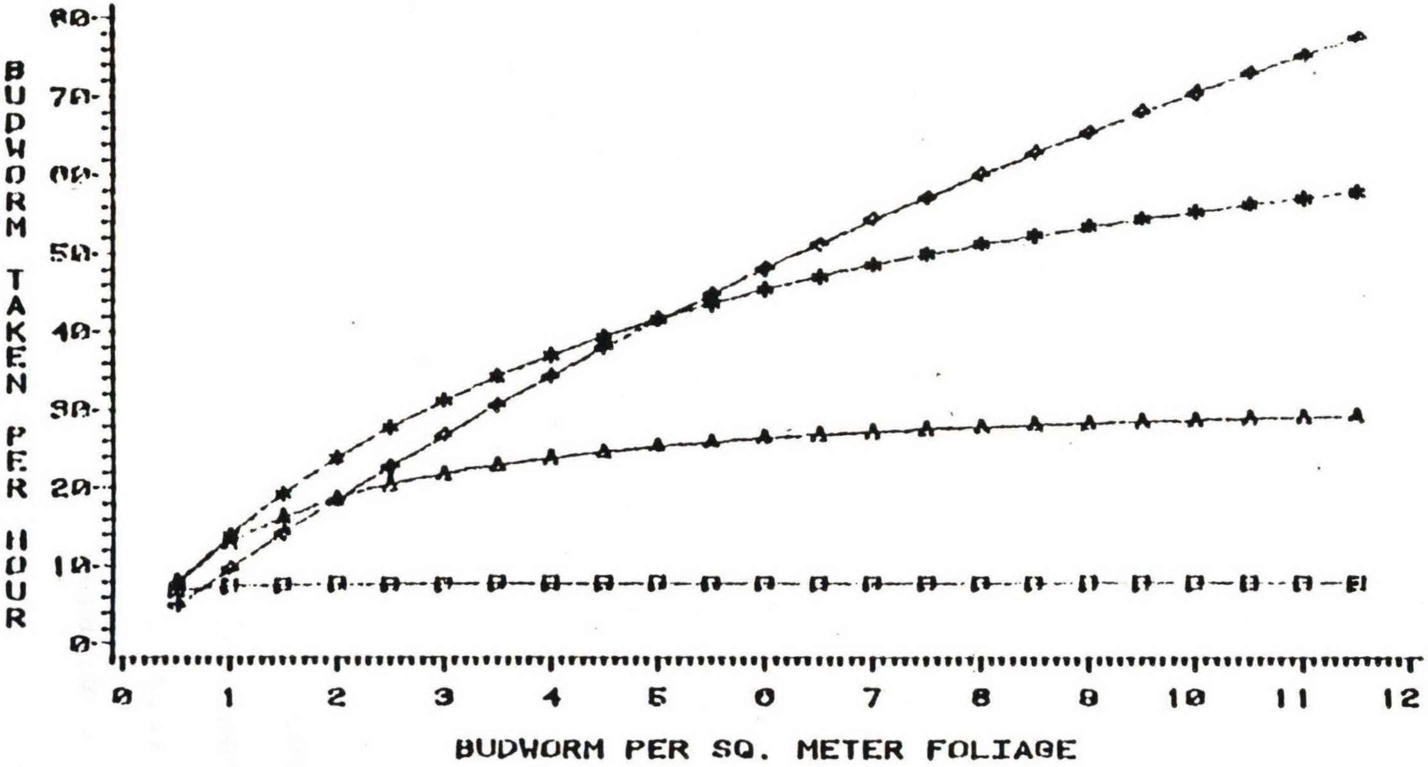


Figure 9. Functional response of chipping sparrow (□), evening grosbeak (◇), pine siskin (✦), and western tanager (△) on budworm in laboratory foraging trials.

densities. Predictions from the Holling model indicate that evening grosbeaks may consume up to 2.6 times more budworm than pine siskins at pandemic density levels. The difference in consumption predicted for higher density levels may be an indication of the capacity of each species for consuming budworm. The grosbeak which weighs 50.0g is much larger than the siskin at 12.1g. An estimate of potential consuming biomass (Salt 1957) based on the weight of a predator predicts nearly the same ratio of consumption (2.7) between these two species as the laboratory trials do.

However, relative consumption measures based on weight are not necessarily good indications of potential consumption between different guilds of birds. The 29.0g western tanager weighs much more that the pine siskin but consumes less. The pine siskin appears to have a more energetic search behavior pattern than the sedentary western tanager. The pine siskin searches by examining the tips of each branch while the tanager sits in one position and scans the branches for prey.

Laboratory versus Field Data

Budworm consumption based on digestive tract contents was found to be much lower than consumption in laboratory trials (Figure 5-8). Three major reasons account for the differences seen:

1) Birds may reach a satiation point after which they spend

their time in nonforaging activities.

2) Birds must spend a portion of their time in other nonforaging behavior associated with reproduction such as in territory defense or nestbuilding.

3) Alternate prey are available in the field which decreases the time birds forage for budworm.

Birds may require a digestive pause between prey items to allow them to process the insects from their bills and esophageal passageway into their gizzards. They may also be limited in terms of digestive passage rate as food items are digested in the gizzard and intestinal tract. Satiation then may explain why the observed handling times in laboratory trials differed from model predictions. The species may have required a digestive pause so the handling time predicted by the model included a "hunger threshold delay" (Holling 1959). In this case,

$$T= T(s)+T(h)+T(d1)$$

and the response function was actually,

$$N=\frac{aTX}{1+a(h+d1)X} \qquad (6)$$

where d1= hunger threshold delay. Handling times observed and predicted for the evening grosbeaks from laboratory trial data were closer than compared to the other species. This bird is much larger than the others and may be able to consume more budworm than the other species before becoming sated.

Satiation in terms of a digestive passage rate delay may also decrease consumption. It may be a factor in consumption as follows:

$$N=\frac{aTX}{1+a(h+d1+d2)X} \qquad (7)$$

where d2= digestive passage rate delay. A predator's ability to digest prey may limit consumption at higher prey densities.

The functional response estimated from collection data also includes nonforaging time since digestive tract contents are a measure of a certain time period whether or not a bird constantly forages. Birds spend a proportion of time in reproductive effort and also foraging for other prey even when the density of budworm is very high (Schluter 1981). Thus, under given environment conditions with alternate prey:

$$(P)T=T(s)+T(h)+T(d1)+T(d2) \qquad (3)$$

where P= the fraction of time spent nonforaging or foraging for other prey. Thus, the Holling model would be:

$$N=\frac{a((P)T)X}{1+a(h+d1+d2)X} \qquad (9)$$

Laboratory trials were used to examine potential consumption by a species if budworm alone were available and nonforaging time was excluded. The number of budworm consumed based on collection data divided by the potential consumption found in the laboratory trials estimates the fraction of time the birds spend foraging for budworm at different densities (Figure 10).

The chipping sparrow exhibits the same consumption in laboratory trials and in the field indicating that in both cases a digestive pause threshold may limit its consumption of budworm. Each of the other species spent decreasing amounts of time foraging for budworm as budworm density increased. The western tanager spent very little of its time foraging for budworm. Insectivorous species like the tanager are generalists in terms of insect consumption (Martin _et_ _al._ 1951) and probably expend less energy foraging for other mobile insect prey than the flocking birds.

Management Implications

The number of budworm consumed in one breeding season by an avian predator may be estimated by finding the product of budworm consumed per hour at a given density, $N(X)$, and the number of hours budworm are available for consumption during a year. Budworm are vulnerable as larger larvae for approximately 55 days in the Pacific Northwest (Robert W. Campbell, pers. comm.). Assuming that an average summer day has 16 hours of daylight, a bird may forage for budworm

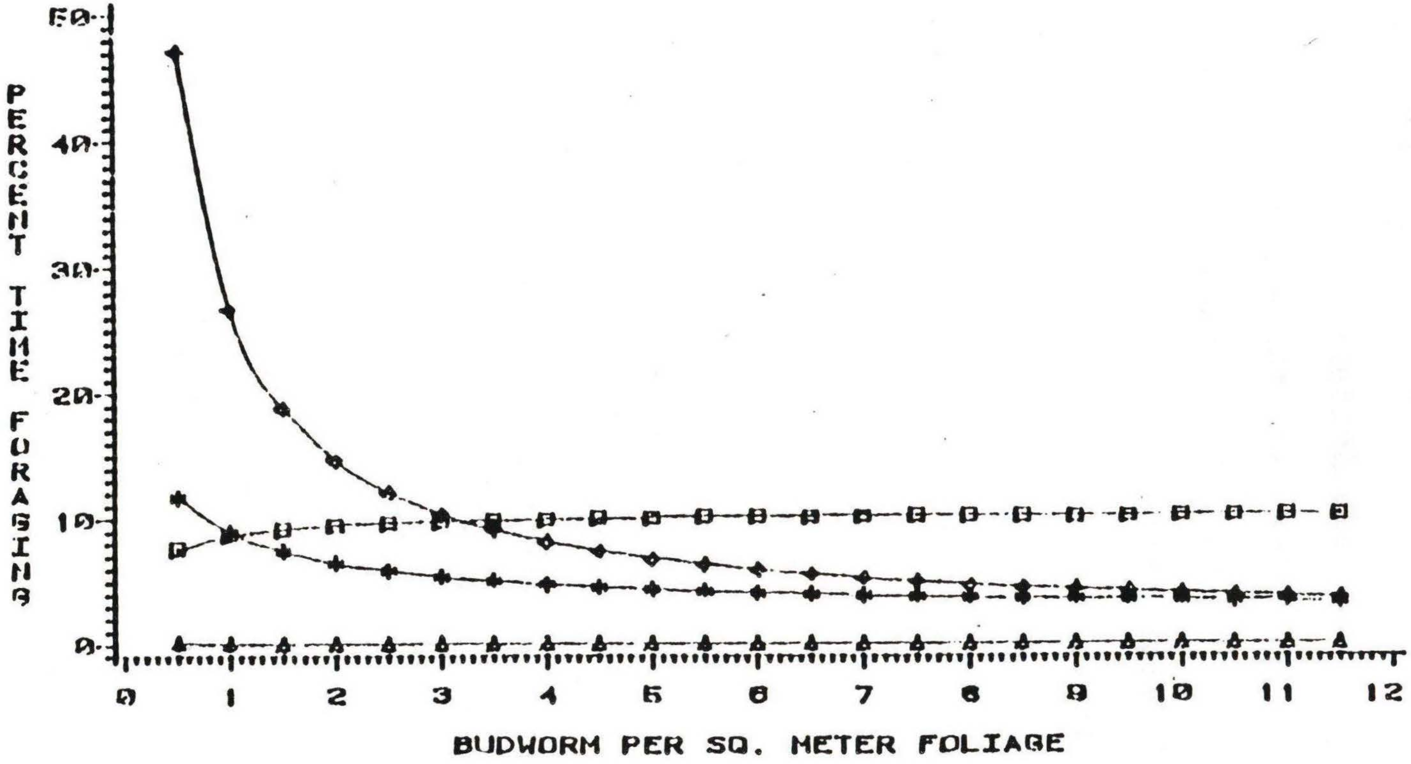


Figure 10. Percent of time spent foraging for budworm for chipping sparrow (□), evening grosbeak (◇), pine siskin (✱), and western tanager (△). The fraction of time birds spent foraging for budworm was calculated based on their consumption of budworm in laboratory foraging trials (all time spent searching for budworm) compared to consumption based on stomach contents.

during 880 hours of the summer.

Avian predators may consume large quantities of budworm in one year (Table 9). Laboratory foraging trials results indicate that resident birds such as the chipping sparrow and western tanager may consume 7400 and 29,000 budworm respectively. Researchers studying avian predators of eastern spruce budworm (*C. fumiferana*) outbreaks reported that one pair of resident birds with three nestlings had the potential to consume 14,000 to 16,000 budworm larvae in one breeding season (Kendeigh 1947, George and Mitchell 1948). Mitchell (1952) calculated that foliage insectivores -- like the tanager -- could consume 20,000 budworm per acre per year.

The flocking species, the pine siskin and evening grosbeak may consume 2 to 6 times as many budworm as the western tanager and 10 to 25 times more budworm than the chipping sparrow (Table 9). Consumption indicated by stomach analysis is much lower because stomach contents reflect availability and consumption of other prey and the amount of time birds spend in reproductive efforts.

Digestive tract contents, however, do not represent all of the prey a bird takes. Predation rates may be underestimated because most birds take as much budworm as they consume to feed each offspring (Gage *et al.* 1970). An adult with three young would consume enough for itself but also would take one-and-one-half times more budworm for its young (Gage *et al.* 1970). Actual consumption by birds

Table 9. Predicted budworm consumption per year by an individual predator based on laboratory foraging trials (and collection data).

SPECIES	Budworm Consumed per year based on laboratory foraging trials (and collection data)						
	Budworm Density (Budworm/m^2)						
	Endemic			Epidemic			High Epidemic
	1	5	10	20	40	80	160
Chipping sparrow	6570	6970	7020	7050	7060	7070	7070
	(5740)	(7010)	(7210)	(7320)	(7370)	(7400)	(7410)
Evening grosbeak	8480	36500	62140	95810	131390	161360	182130
	(22630)	(24780)	(25100)	(25250)	(25330)	(25370)	(25390)
Pine siskin	12230	36610	48770	58490	64950	68750	70820
	(10950)	(16020)	(17010)	(17510)	(17830)	(17970)	(18040)
Western tanager	11430	22340	25360	27210	28230	28770	29050
	(1080)	(1360)	(1410)	(1430)	(1440)	(1450)	(1450)

during the breeding season would be at some level between the values indicated by laboratory trials and stomach contents.

Based on our findings, we believe birds have a substantial role in the control of budworm populations. Different bird species have different functional responses and effectiveness at regulating the population of their prey. The density at which a predator is no longer contributing to stabilize an insect population can be derived for 'S' shape (Type III: Holling 1959) functional responses (Oaten and Murdoch 1975), but not for continually decreasing responses (Type II) which we found for birds foraging on budworm. However, as a species asymptotically approaches maximum consumption along a Type II curve, it reaches a point where it no longer consumes more prey as prey density increases. At this point, predation by a species drops off dramatically.

The density of budworm at maximum consumption cannot be calculated because the response is asymptotic, but the density can be calculated at some arbitrary point (90 percent) near the maximum. This point was examined for the species examined here and was found to be at low endemic levels for the chipping sparrow, low-epidemic levels for the tanager, mid-epidemic levels for the pine siskin, and pandemic levels for the evening grosbeak (Table 5).

Morris _et al._ (1958) noted that in the eastern U.S., at low budworm densities of 1000 budworm per acre, 2 pair of resident birds consuming budworm in 2 percent of their diet could keep the population from growing. Potential consumption for the flocking species we studied is much higher, and therefore, their ability to regulate budworm populations should be much greater.

The preference birds show for larger budworm (Table 7-8) implies that they have a larger contribution to mortality than might be expected if they took prey randomly. Budworm population fluctuations are most closely linked to mortality of the larger larval stages (Morris _et al._ 1958). Selective foraging by birds on larger budworm ultimately magnifies their effect on the growth of the insect population.

LITERATURE CITED

Bent, A.C. 1968. Life histories of birds. Dover Publ. Inc. NY.

Blais J.R. and G.H. Parks 1964. Interaction of evening grosbeak (_Hesperiphona_ _vespertina_.) and spruce budworm (_Choristoneura_ _fumiferana_ (Clem.)) in a localized outbreak treated with DDT in Quebec. Can. J. Zool. 42:1017-1024.

Bruns, H. 1960. The economic importance of birds in the forest. Bird Study 7(4):193-208.

Buckner, C.H. 1966. The role of vertebrate predators in the biological control of insects. Ann. Rev. Entomol. 11:470-499.

-----. 1970. The role of vertebrates in the integrated approach to control. USDA, Forest Service Insect and Disease Lab., Hamden, Conn.

Franz, J.M. 1961. Biological control of pest insects in Europe. Ann. Review of Entomol. 6:183-200.

Gage, S.H., C.A. Miller, and L.J. Mook. 1970. The feeding response of some forest birds to black-headed budworm. Can. J. Zool. 48:359-366.

Garton, E.O. 1981. Impact and management of vertebrate predation on western spruce budworm. Proposal to Canada/U.S. Spruce Budworm Project West. 78pp. (unpubl.)

Gause, G.F. 1934. THe struggle for existence. WIlliams and WIlkens Co. Baltimore.

George, J.L. and R.T. Mitchell 1948. Calculations on the extent of spruce budworm control by insectivorous birds. J. Forestry 46:454-455.

Goss-Custard, J.D. and P. Rothery 1976. A method for measuring some components of foraging of certain birds in the field. Anim. Behav. 24:545-550.

Griffiths, K.J. 1969. The importance of coincidence in the functional and numerical responses of two parasites of the European pine sawfly, Neodiprion sertifer. Can. Entomol. 101:573-713.

Hagen, K.S., R. van den Bosch, and D.L. Dahlsten 1971. The importance of naturally-occurring biological control in the western United States, pp. 253-293 in C.B. Huffaker (ed.). Biological Control. Plenum Press, NY. 511pp.

Hardman, J.M. and A.L. Turnbull. 1974. The interaction of spatial heterogeneity, predator competition and the functional response to prey density in a laboratory system of wolf spiders (Araneae: Lycosidae) and fruit flies (Diptera: Drosophila). J. Anim. Ecol. 43:155-171.

Herberg, M. 1965. Bird protection for control of injurious insects and its results. AnzSchadlingk 38pt. 9pp. (Summary in 1967 Rev. Appl. Entomol. 55:497).

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91:385-398.

Jackson, J.A. 1979. Insectivorous birds and North American forest ecosystems, pp.1-7 in J.G. Dickson, R.N. Conner, R.R. Fleet, J.C. Kroll, and J.A. Jackson (eds.). The Role of Insectivorous Birds in Forest Ecosystems. Academic Press, NY. 381pp.

Kendeigh, S.C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Canadian Dept. of Lands and Forests Biol. Bull. No.1, Ontario. 100pp.

Lotka, A.J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore.

Marquardt, D.W. 1963. An algorithm for least-squares estimation of nonlinear parameters. J. Soc. Indust. Appl. Math. 11(2):431-441.

Martin, A.C., H.S. Zim, and A.L. Nelson 1951. American wildlife and plants: a guide to wildlife food habits. Dover Publications, NY. 500pp.

Mitchell, R.J. 1952. Consumption of spruce budworm by birds in a Maine spruce-fir forest. J. Forestry 50:387-389.

Morris, R.F., W.F. Cheshire, C.A. Miller, and D.G. Mott 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39:487-494.

Murton, R.K., A.J. Isaacson, and N.J. Westwood 1963. The feeding ecology of the woodpigeon. Br. Birds 56:345-375.

Nicholson, A.J., and V.A. Bailey. 1935. The balance of animal populations. Proc. Zool. Soc. London. Part I:551-598.

Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization availability data. J. Wildl. Manage. 38(3):541-545.

Oaten, A., and W.W. Murdoch. 1975. Functional response and stability in predator-prey systems. Amer. Natur. 109(967):289-298.

Otvos, I. 1979. The effects of insectivorous bird activities in forest ecosystems: an evaluation, pp.341-374 in J.G. Dickson, R.N. Conner, R.R. Fleet, J.C. Kroll, and J.A. Jackson (eds.). The Role of Insectivorous Birds in Forest Ecosystems. Academic Press, NY. 381pp.

Poznanin, L.P. (ed.) 1956. Ways and means of using birds in combating noxious insects. USDC, Israel program for scientific translations. 138pp.

Salt, G.W. 1957. An analysis of avifaunas in the Teton mountains and Jackson Hole, Wyoming. Condor 59(6):373-393.

Schluter, D. 1981. Does the theory of optimal diets apply in complex environments? AM. Natur. 118:139-147.

SAS Institute 1979. Sas user's guide, 1979 edition.J.T. Helwig and K.A. Council (eds.). SAS Institute Inc. Cary, N.C. 494pp.

Simmons, G.A. 1968. Interrelationships of the chipping sparrow and the jack pine budworm. M.S. Thesis, Michigan Tech. Univ. 50pp.

Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35.

-----. 1964. Analysis of processes involved in the natural control of insects. In J.B. Cragg (ed.), Advances in ecological research. Vol. 2. Academic Press, London. 264pp.

Takekawa, J.Y., E.O. Garton, and L.A. Langelier. 1982. Biological control of forest insect outbreaks with avian predators. Proc. 47th Amer. Wildl. Conf. (in press).

Thomas, J.W., G.L. Crouch, R.S. Bumstead, and L.D. Bryant 1975. Silvicultural options and habitat values in coniferous forests, pp.272-287, in D.R. Smith (ed.), Proceedings of the symposium on management of forest and range habitats for nongame birds. USDA, USFS, Gen. Tech. Rept. WO-1, 343 pp.

U.S. Forest Service 1976. Cooperative western spruce budworm control project. Pacific Northwest Region Rept. 18pp.

Volterra, V. 1926. Variazioni efluttuazioni del numero d'individi in speci animali conviventi. Mem. Accad. Lincei 2:31-113.

Ware, D.M. 1972. Predation by rainbow trout (Salmo gairdneri): the influence of hunger, prey density and prey size. J. Fish. Res. Board Can. 29:1193-1201.

Watt, K.E.F. 1959. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. Can. Entomol. 91: 129-144.

Wiens, J.A. 1975. Avian communities, energetics, and functions in coniferous forest habitats, pp.226-261, in D.R. Smith (ed.), Proceedings of the symposium on management of forest and range habitats for nongame birds. USDA, USFS, Gen. Tech. Rept. WO-1, 343pp.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, N.J. 620pp.

SECTION TWO

Economic Evaluation

HOW MUCH IS AN EVENING GROSBEAK WORTH?

John Y. Takakawa and Edward O. Garton

Abstract: Many natural resource decisions are made by evaluating the benefits and costs of different management alternatives. Our studies on avian predators of the western spruce budworm suggest that a minimum dollar value may be assigned to passerines based on their role as budworm predators. Bird predation is sufficient to reduce timber growth losses in stands infested with budworm. We estimated the economic value of this predation on two stands in north-central Washington by assessing the cost to substitute aerial spraying with insecticides for bird-caused mortality. It would cost a minimum of \$3770/mi^2/yr to duplicate the effect of birds in these stands. This figure can be used to appraise the value of individual species which are important predators such as the evening grosbeak, to evaluate the cost-effectiveness of biological control, and to assess the costs and benefits of silvicultural practices affecting the avian component of forest communities.

On federal lands, administrative decisions are guided by benefit-cost analyses which identify management alternatives that maximize the value of the land for society. Benefit-cost analyses require reasonable, quantitative estimates of benefits and costs associated with proposed alternative actions. Natural resources such as wildlife are difficult to assign a value to because wildlife values are based upon esthetics or other intangible assets that are hard to quantify in dollar terms. As a result, the wildlife resource is often undervalued or neglected in federal land management decisions.

For example, passerines are abundant and ubiquitous species in forest communities, yet they are rarely evaluated in benefit-cost analyses because their value is difficult to appraise. Our work on avian predators of the western spruce budworm (Choristoneura occidentalis) suggests that passerines play a very valuable role in controlling outbreaks of this damaging forest insect, and our objective is to demonstrate how their value as predators might be quantified.

A 5-year research project on the western spruce budworm is being conducted jointly by the Canadian and U.S. Forest Service (CANUSA) to investigate the biology, population dynamics, and management of this important forest insect pest. The budworm is a larval defoliator of Douglas-fir (Pseudotsuga menziesii), true firs (Abies spp.) and spruce (Picea spp.). Its life cycle begins in the fall when the female moths deposit their eggs on conifer needles. Within 10 days, the budworm emerge as small larvae and overwinter under bark scales. In the following summer, the larvae consume new needles and buds and grow to over 2.5 cm in length. The larvae pupate in the fall and complete the cycle with adult flight (USFS 1976).

The budworm problem was first identified in the 1940's when outbreaks led to defoliation of large areas of forest in the northeast. Approximately 36.4 million hectares (90 million acres) of forest are infested by the budworm in the U.S., and more lands have been sprayed for the budworm than for any other forest insect (USFS 1976).

Our study of avian predators of the budworm is part of the research effort identifying natural enemies of the budworm. The goal of this research is to determine the role of natural enemies in budworm population dynamics and to suggest how they might be used in an integrated pest management plan. Our work focuses on the larval and pupal stages of the budworm from late May through early August. This period is critical for the reproduction of both the budworm and its avian predators (Morris *et al.* 1958).

Study Areas and Methods

Budworm outbreaks in the early 1970's on the eastern slopes of the Cascade range in north central Washington led to selection of the Methow and Twisp River drainages as sites for budworm population dynamics studies (USFS 1976).

When we began our study in 1979, both areas had light to medium defoliation with late instar larval densities of 52 (Methow River) and 48 (Twisp River) insects per square meter of foliage (R.W. Campbell, pers. comm.).

We set up two bird census plots overlaying 5-hectare entomological study plots established one year earlier. An 11.25-hectare plot was gridded at the Twisp River site (No. 3) while steep topography limited our Robinson Creek plot along the Methow (No. 2) to 9.4 hectares. Both plots were predominantly Douglas fir and ponderosa pine (*Pinus ponderosa*). The Robinson Creek plot was heavily stocked with smaller trees while the Twisp River plot contained a heterogeneous mixture of small and large trees separated by openings with dense shrub cover.

Censusing was conducted during the breeding season on 10 different mornings along 6 450-meter transect lines. Censuses began at daybreak and lasted for 3 hours. A perpendicular distance estimate was recorded for each bird or group of birds sighted. Densities of groups were estimated by a Fourier series line transect model for each abundant species (Burnham *et al* 1980). Densities of less abundant species were estimated following Emlen's procedure (Emlen 1971).

Birds were collected for stomach analysis in areas adjacent to our study plots. Each digestive tract was placed in 70% alcohol within 15 minutes of collection to prevent deterioration of the contents. In our laboratory, the stomachs were examined with a dissecting microscope. All whole budworm larvae and pupae, larval mandibles, and pupal cremasters were recorded to provide estimates of budworm consumed by individual birds. Digestion trials were also run in the laboratory on birds captured for foraging trials. A nontoxic dye was injected into budworm that were fed to the birds to determine the passage rate of budworm through the digestive tracts of the birds.

Standard errors for estimates based upon the product of two or more variables (e.g. total density, total consumption per bird) were calculated following the approach of Goodman (1960). Each variable was assumed to be independent and normally distributed.

Density of Grosbeaks

Nearly every species censused in 1979 was documented to be a predator on budworm (Table 1). One abundant and particularly voracious budworm predator was the evening grosbeak (*Hesperiphona vespertina*), a flocking bird with a large bill adapted for seed eating (Bent 1947). To estimate the extent of grosbeak predation, the number of grosbeaks and the number of budworm eaten per bird were calculated.

The density of grosbeaks was estimated by multiplying the density of grosbeak groups censused on one plot (Table 1) by average group size and by a correction factor for

Table 1. Density of major avian predators and their potential for consumption. Densities were calculated with Emlen's procedure (Emlen 1971) or with a Fourier model (Burnham et al. 1980). Potential consumption was estimated by total consuming biomass (Consuming biomass = (mean weight in grams)$^{.7}$: Salt 1957).

Species	Site 2		Site 3	
	[1]Density (SE) (Birds/km^2)	Consuming Biomass(g)	[1]Density (SE) (Birds/km^2)	Consuming Biomass(g)
Chestnut-backed Chickadee	—	—	10.2 (4.78)	54.7
Mountain Chickadee	21.3 (6.64)	121.2	23.1 (6.25)	131.4
Cassin's Finch	—	—	[2]36.4 (6.36)	371.3
Hammond's Flycatcher	[2]45.2 (14.18)	267.6	[2]28.0 (10.58)	165.8
Evening Grosbeak	[2]83.2 (21.03)	1379.0	[2]512.1 (48.90)	7917.1
Dark-eyed Junco	9.5 (3.00)	71.0	[2]24.1 (7.31)	180.0
Ruby-crowned Kinglet	—	—	4.9 (1.47)	21.0
Red-breasted Nuthatch	—		13.0 (2.05)	65.7
Western Wood Pewee	7.4 (2.00)	46.9	13.7 (2.80)	86.9
American Robin	10.5 (3.24)	241.2	—	—
Pine Siskin	13.9 (6.06)	79.6	[2]82.1 (15.61)	470.4
Chipping Sparrow	46.3 (9.05)	266.7	[2]121.6 (21.46)	700.4
Western Tanager	34.3 (7.20)	362.2	[2]28.2 (5.86)	297.8
Swainson's Thrush	14.7 (6.60)	158.9	31.5 (3.90)	340.5
Solitary Vireo	14.8 (6.61)	80.8	4.3 (0.94)	23.5
MacGillivray's Warbler	—	—	21.3 (3.45)	99.3
Nashville Warbler	12.3 (3.68)	52.8	—	—
Townsend's Warbler	—	—	27.3 (3.46)	155.3
Yellow Warbler	—		16.0 (3.19)	78.4
Yellow-rumped Warbler	7.4 (3.13)	44.8	23.1 (4.97)	139.8
TOTAL	320.8 (92.42)	3172.7	1020.9 (153.34)	11299.3

[1] Density of major avian predators sighted 10 or more times.

[2] Fourier series estimate (25 or more sightings).

young of the year. Mean group size was determined from visual records. On site 2, group size was 1.36 (SE=.133), slightly lower than site 3 at 1.62 (SE=.064). The correction factor must be included to account for fledglings which were not censused on the line transects. Skutch (1946) noted in his nestling studies that young birds consume as much as adults during the breeding season. Thus, one censused bird represents itself and half of its offspring. For example, grosbeaks rear an average of 3.5 young so that one grosbeak sighted during a census represents 2.75 birds (Harrisson 1979, Gage _et al._ 1970).

However, grosbeaks are regurgitative feeders so that digestive tracts collected during the 14-day nestling period contain prey for both the bird and its young. Also, during the 14-day incubation the female is fed by the male. Therefore, for 28 days of the 55-day period when budworm are vulnerable to avian predation, grosbeak juveniles are not consuming budworm or are represented by increased budworm in the esophagus of the adults. For the rest of the summer, juveniles must be accounted for. The correction for the number of grosbeaks actively consuming prey per censused bird would be 2.75 x (27 / 55) = 1.35. Therefore, the total number of grosbeaks consuming budworm was 115 grosbeaks / km^2 at Robinson Creek (SE = 50) and 707 grosbeaks / km^2 at Twisp River (SE = 233).

Budworm Consumed by Grosbeaks

The average consumption by one grosbeak was calculated from stomach samples. The number of budworm per stomach was divided by the digestive passage rate (1.2 h,SE=.08) to convert consumption to budworm per hour. To estimate budworm consumption through one summer, a 16-hour day was assumed over the 55-day period of budworm availability. Based on the average number of budworm per stomach, 36.2 (SE = .54) at site 2 and 17.4 (SE = 1.58) at site 3, an individual grosbeak consumed from 12,600 budworm on site 3 (SE = 5240) to 26,400 budworm on site 2 (SE = 9020) in 1979.

Total budworm consumption is the product of the number of birds and the budworm consumed per bird. In 1979, total evening grosbeak predation over a square kilometer was estimated to be 3,036,000 budworm on site 2 (SE = 1,761,000) and 8,900,000 on site 3 (SE = 4,900,000).

Estimating the Benefit of Avian Predation

The number of budworm that grosbeaks consume on our study areas strongly suggests that avian predators play a significant role in reducing defoliation damage. Since radial growth of a conifer depends on the amount of foliage on the tree (Mitchell 1975), bird predation may be preventing timber growth losses caused by budworm defoliation. We therefore posed the question, what is the value of this avian predation?

One approach to assessing the value of avian predation is through substitution. Assuming birds were removed from a stand, just what would it take to duplicate their mortality effect on budworm in the stand? The current control measure most widely used by managers is aerial application of pesticides. Spraying costs may be used to calculate a substitution value for avian predators of the budworm.

The Value of the Bird Community

On our study areas, cooperators Torgerson and Campbell (1981) compared branches excluded from bird predation to control branches (Table 2). Exclosure cage experiments showed that budworm survival was significantly decreased by 71% (site 2) to 73% (site 3) on control branches compared to branches where birds were excluded.

On the Okanogan National Forest, spraying with sevin-4-oil, a widely used insecticide, was shown to decrease budworm survival by 80% when treatment and control plots were compared (Mounts *et al* 1978). The cost of spraying may be substituted for the value of avian predation because spraying to decrease the budworm population by 80% has a positive benefit-cost ratio in this area (USFS 1977). Assuming that the mortality rates caused by birds and

Table 2. Mortality caused by birds based on experimental results using exclosure cages (Torgerson and Campbell 1981). Budworm densities were recorded as budworm per 100 shoots of new foliage.

Site 2	$\bar{X}$	SE	N
Control	2.0	0.42	20
Protected from birds	5.9	1.42	10
% Mortality	$1 - \frac{\text{control}}{\text{protected}}\ (100) = 71\%$		

Site 3	$\bar{X}$	SE	N
Control	1.3	0.49	20
Protected from birds	4.4	4.25	10
% Mortality	$1 - \frac{\text{control}}{\text{protected}}\ (100) = 73\%$		

spraying remain constant over five years, the cumulative mortality caused by birds would be duplicated by spraying with insecticide in four of the five years. The value of avian predation would be 80% of the annual cost to spray.

Spray costs to replicate the mortality birds cause over a 100-hectare area (1 km^2) would be $1820.00 per year (USFS 1977). Therefore, the effect songbirds have as predators of the budworm is worth a minimum of 80% of that value or $1460.00 / km^2/yr ($3770.00 / mi^2 / yr).

The Dollar Value of One Grosbeak

To compute the value of one grosbeak, we must estimate what portion of the total budworm mortality caused by birds was due to grosbeaks. Grosbeaks constituted 43% of the avian predator consuming biomass at site 2 and 70% at site 3 (Salt 1957: Table 1). Grosbeak consumption of budworm was therefore worth $620.00 at site 2 and $1020.00 at site 3. When the number of grosbeaks on each site is considered, the predation value of one grosbeak was equivalent to investing $1.40 (site 3) to $5.40 (site 2) in spraying costs depending on the site.

Discussion

We have shown that birds have a value as predators of the western spruce budworm. If birds can suppress budworm outbreaks by keeping pest populations at low density levels, they may have a much greater value than we reported. The point estimate derived for bird value in this analysis has limited usefulness, but with further refinement, our findings may have wider application.

The density of birds and the amount taken by an individual varies with the density of budworm. Using data collected from several sites in 4 states (Washington, Idaho, Oregon, and Montana), we will model the numerical and functional responses of the avian predators and estimate mortality caused by birds at different budworm densities. Once the budworm simulation model is completed, we should be able to appraise the value of birds over a wide range of budworm densities. This estimate will include their long-term effect on the frequency and duration of budworm outbreaks.

Conclusions and Implications for Management

The technique of assigning a dollar value to bird populations could be a useful way to critically evaluate the feasibility of biological control management. Avian predator management would be economically profitable up to the point where the marginal benefit of adding birds equals the marginal cost (Leftwich 1970). Silvicultural techniques, habitat management, and direct manipulations of limiting resources (i.e. providing nest boxes, water sources) could be applied to maximize the consuming biomass of avian predators. Current European forest practices include management for passerines. Several studies have indicated that bird densities can be manipulated (Campbell 1968, von Haartman 1957). Considering the detrimental side effects of pesticides on insect predators, parasites, and on the environment, more research should be directed at studying ways to manage natural enemies of forest insects.

Using economic analyses to assess the value of our wildlife resources will lead tc more objective management decisions. By quantifying benefits associated with wildlife species, their significance as members of complex ecosystems may be realized. At the very least, assigning a dollar figure to a wildlife species to explain a portion of its worth will decrease the amount of its value which remains intangible.

Literature Cited

Bent, A.C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Dover Publ. Co., N.Y. 602 pp.

Burnham, K.P., D.R. Anderson, and J.L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. No.72. 202 pp.

Campbell, B. 1968. The Dean nestbox study, 1942-1964. Forestry 41:27-28.

Emlen, J.T. 1971. Population densities of birds derived from transect counts. Auk 88:323-342.

Gage, S.H., C.A. Miller, and L.J. Mook. 1970. The feeding response of some forest birds to black-headed budworm. Can. J. Zool. 48:359-366.

Goodman, L.A. 1960. On the exact variance of products. J. Amer. Statist. Assoc. 55:708-713.

Harrison, C. 1978. Nests, eggs, and nestlings of North American birds. Collins, Sons and Co., Great Britain. 416pp.

Leftwich, R.H. 1970. The price system and resource allocation, 4th ed., Dryden Press Inc., Hinsdale, Ill. 402pp.

Mitchell, K.J. 1975. Dynamics and simulated yield of Douglas-fir. Forest Science Monogr. No. 17. 39pp.

Morris, R.F., W.F. Cheshire, C.A. Miller, and D.G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39:487-494.

Mounts, J., R.E. Dolph, D. McComb, and T.F. Gregg. 1978. 1977 western spruce budworm control program. USDA, USFS, R6. 33pp.

Salt, G.W. 1957. An analysis of avifaunas in the Teton mountains and Jackson Hole, Wyoming. Condor 59:373-393.

Skutch, A.F. 1946. The parental devotion of birds. Scientific Monthly 63:327-362.

Torgerson, T.R., and R.W. Campbell. 1981. Some effects of avian predators on the western spruce budworm in north-central Washington. Environmental Entomol. (in press).

U.S. Forest Service 1976. Cooperative western spruce budworm control project. USDA, U.S. Forest Service, Pacific Northwest Region, 18pp.

____________________ 1977. 1977 final environmental statement addendum to the final 1976 cooperative western spruce budworm pest management plan. USDA, U.S. Forest Service, Pacific Northwest Region, FES(Adm)-76-7.

von Haartman, L. 1956. Territory in the pied flycatcher. Ibis 98(3):461-475.

SECTION THREE

Reprinted from: Transactions of the 47th North American Wildlife and Natural Resources Conference, 1982.
Published by the Wildlife Management Institute, Washington, D.C.

Biological Control of Forest Insect Outbreaks: The Use of Avian Predators

John Y. Takekawa, Edward O. Garton, and Lisa A. Langelier
Department of Wildlife
College of Forestry, Wildlife, and Range Sciences
University of Idaho, Moscow

Biological control of destructive forest insects involves managing natural enemies of the insect to control or regulate its population below an economically significant damage level. There has recently been a growing interest in the potential of biological control as an alternative to pesticides. This shift in emphasis has resulted following recognition of deleterious side effects associated with pesticide use.

Two major problems of the continual use of pesticide are the evolution of genetically resistant strains of insects and mortality of nontarget organisms, including natural enemies (Rudd 1964, Miller and Varty 1975, Varty 1975, Comins 1979). Intensive forest management has created homogeneous environments favorable for the rapid increase and spread of insect populations (Hagen et al. 1971). The use of pesticides within these forests may prolong insect outbreaks and shorten the period between eruptions (Blais 1974, Holling et al. 1979).

Predators, parasites, and pathogens may contribute significantly to the control of pest populations (Poznanin 1956, Bruns 1960, Franz 1961, Herberg 1965, Buckner 1966, Buckner 1970, Thomas et al. 1975, Wiens 1975). Birds are known to be important predators of destructive forest insects (Table 1). Eighty percent of prey in the diet of insectivorous birds in Russian forests were classified as damaging pest species (Poznanin 1956). Additionally, birds are selective in their consumption of insects. They have been reported to select for nonparasitized individuals (Franz et al. 1955, Korl'kova 1956, Buckner and Turnock 1965, Coppel and Sloan 1971, Sloan and Simmons 1973, Schlichter 1978), and they also aid in the dispersal of viruses (Franz et al. 1955, Entwistle et al 1977a, Entwistle et al. 1977b). Thus, in many instances birds have been reported to add to natural mortality without greatly decreasing the effect of other natural enemies.

In this paper, we will show that avian predation is a desirable and feasible approach for insect pest management. Management strategies for implementing biological control will be discussed.

The Case for Biological Control

Insect populations have an innate capacity for tremendous growth within a short time period. One pair of potato beetles could produce 60 million offspring in one season, and one pair of houseflies could produce 91 trillion offspring in just five months (Henderson 1927). Therefore, effective control requires maintaining a very high level of mortality. For example, female adults of the western spruce budworm (*Choristoneura occidentalis*) produce an average of 66 female offspring (R. W. Campbell, unpubl. data). Natural mortality factors must eliminate 65 of the 66 female offspring or 98.5 percent annually to prevent population increases.

Mortality factors that control insect populations are classified as density-independent factors such as site characteristics, climate, and weather, and density-dependent factors, including natural enemies. Density-independent factors are nonregulatory because they cause a constant level of mortality over varying insect densities (Huffaker et al. 1971). Density-dependent factors may exert a regulatory pressure on a population by increasing in effectiveness as an insect increases in abundance. This type of relationship is exhibited by many natural enemies and has been termed a negative-feedback loop (Hagen et al. 1971).

Reliable biological control agents are identified by four characteristics: (1) adaptability to different environments or changing conditions, (2) an ability to search a large area, implying good mobility, (3) a large power of increase relative to the prey, and (4) other characteristics specific to the prey (Huffaker et al. 1971).

Avian predators have all of these qualities except the ability to reproduce as quickly as their prey (Morris et al. 1958). Birds are able to survive in areas without high concentrations of one particular pest insect. They may therefore be able to prevent outbreaks more readily than other natural enemies, such as parasites or pathogens, which tend to be very host-specific. Flocking species such as evening grosbeaks (***Hesperiphona vespertina***) concentrate at locations where insects are very abundant. Their intensive predation may shorten the duration of outbreaks (Blais and Parks 1964).

The regulating effect exerted by avian predators may be separated into two density-dependent responses (Solomon 1949, Holling 1959). A functional response is seen when the number of insects one bird consumes increases as the density of insects increases. A numerical response is seen when the number of predators increases as the density of insects increases. This response may be seen immediately through migration, but it is also seen after a time lag following higher reproduction or survival of young. The total response of a bird to an insect is the product of its functional and numerical responses.

Many researchers have documented the importance of avian predators in the control of destructive insects (Table 1). Songbirds may respond strongly to increases in the abundance of their prey (Morris et al. 1958, Gage et al. 1970, Koplin 1972, Morse 1978). Avian predation is very important at endemic levels, contributing at epidemic densities, and ineffectual under pandemic conditions in the control of insect pests (Thomas et al. 1975).

The effectiveness of birds at regulating forest insects at low, endemic levels has not been studied. Their potential role in preventing outbreaks remains unknown. Studies at low insect densities are lacking because the insects are extremely difficult to census with a reasonable precision. Studying avian predation at low prey density levels requires prolonged exclusion of birds from a large area to see if the frequency of outbreaks increases without birds.

Most of the evidence indicating that birds are beneficial in preventing outbreaks is indirect. Documented cases have shown that where birds are artificially increased, outbreaks have been prevented. One forested area in Germany that was supplied with nestboxes remained undamaged while adjacent lands were totally defoliated (Berlepsch 1923). Unmanaged and managed areas were obvious to distinguish in this case because an area managed for holenesting birds located 50 m (164 ft.) from the defoliation zone remained green (Appel and Schwartz 1921). In a similar study, Herberg (1960) found that, over a 33-year period, areas infested by *Bupalus piniar-*

Table 1. Avian predation on destructive insects.

Insect	Density	Stage	Avian predator(s)	% Mortality	Study
LEPIDOPTERA					
Barred red moth			tits, goldcrests	23	Gibb 1960
Barred red moth	epidemic			31	Tinbergen 1949
Black arches moth		larvae		50	Wellenstein 1959
Black-headed budworm	endemic	larvae, pupae		3–14	Gage et al. 1970
Eastern spruce budworm	epidemic	larvae		13–39	Tothill 1923
Eastern spruce budworm	epidemic	larvae		4.3	Kendeigh 1947
Eastern spruce budworm	pandemic	larvae	vireos, fringellids, chickadees	3.5–7.0	George & Mitchell 1948
Eastern spruce budworm	epidemic	larvae		37–45	Dowden et al. 1953
Eastern spruce budworm		larvae	warblers, kinglets, juncos	1.0–6.3	Morse 1978
Jack pine budworm	endemic	larvae, pupae		40–65	Mattson et al. 1968
Jack pine budworm		larvae	chipping sparrow	3.3	Simmons 1968
Western spruce budworm	epidemic	larvae, pupae	evening grosbeak, siskins, crossbills	49–87	Campbell & Torgersen 1982
Codling moth		larvae		27–93	LeRoux 1959
Codling moth		larvae		55–82	Mailloux & LeRoux 1960
Codling moth			woodpeckers	50	MacLellan & McPhee 1971
Codling moth		larvae, pupae	silvereye	53	Wearing 1975
Codling moth	endemic	larvae		95	Solomon et al. 1976
Codling moth		larvae	tits	66	Solomon & Glen 1979
Codling moth		winter larvae	blue tits	95	Glen et al. 1981
Corn earworm & fall armyworm		larvae	starlings	100	Stewart 1973

Table 1. Avian predation on destructive insects. (cont'd.)

Insect	Density	Stage	Avian predator(s)	% Mortality	Study
Douglas-fir tussock moth		larvae, pupae, eggs	nuthatches, chickadees, juncos	19, 19–49, 3–30	Torgersen & Dahlsten 1978
Douglas-fir tussock moth		eggs	mountain chickadee	16.7–71.7	Dahlsten & Copper 1979
Earworms				68	Barber 1942
European corn borer		larvae	grackles, blackbirds, starlings	12–84	Barber 1925
European and Southwestern corn borer		winter larvae		60	Wall & Whitcomb 1964
Southwestern corn borer		winter larvae	flicker	98.3	Floyd et al. 1969
Southerwestern corn borer	epidemic	winter larvae	flicker	64–82	Black et al. 1971
Larch budmoth		larvae	junco, redpolls, chickadees	3–10	Werner 1980
Larch casebearer	endemic	winter cocoons	warblers, kinglets, chickadees	23.5	Sloan & Coppel 1968
Lodgepole needle-miner		larvae	evening grosbeak (only)	10	Dahlsten & Herman 1965
Gypsy moth		pupae	vertebrates	70	Campbell & Sloan 1976
Gypsy moth		larvae		0.4–1.1	Inozemtsev et al. 1980
Gypsy moth & tortrix viridana		larvae	4–10 nestboxes/ha	47.3–80.2	Strokov 1956
Tortrix virdana and Cacoecia crataegana		larvae	without-with nestboxes	1–2.5	Inozemtsev 1976
Pine beauty moth	epidemic		tits, goldcrests	24–34	Gibb 1960
Pine beauty moth	epidemic			32–49	Tinbergen 1949
Pine looper	epidemic		tits, goldcrests	10	Gibb 1960
Pine looper	epidemic			13	Tinbergen 1949
Pine Noctuida		larvae		2.7	Gerasimova & Unterberger 1956
Potato moth	endemic	larvae	western silvereye	66	Springett & Matthiessen 1975

Tobacco hornworm	experiment	larvae	house sparrow	100	Stewart 1969
Tobacco hornworm		larvae		58.5–100	Thurston & Pracherabmoh 1971
Tobacco insects		larvae	crows, gackles, bluebirds	47–56	Stewart 1975
Fall webworm		adults		98	Keve and Reichart 1960
White butterfly			tree sparrow, whitethroats	10–20	Roer 1957
White butterfly				3.7–8.9	Ashby & Pottinger 1974
Winter moth		larvae, female adults	titmice	0.3–2.6, 20	Betts 1955
Lepidoptera		larvae		18–63	Holmes et al. 1979
Lepidoptera		larvae		35–40	Tinbergen 1960
COLEOPTERA					
Ash borer			woodpeckers	67–81	Solomon 1975
Living beech borer		larvae	woodpeckers	39	Solomon 1969
Oak branch borer			woodpeckers	65	Solomon 1977
Poplar borer				12	Tichy 1963
Poplar borer		larvae	woodpeckers	13–65	Solomon 1969
White oak borer			woodpeckers	32	Solomon 1969
Grass grub	epidemic	larvae	starling	40–60	East & Pottinger 1975
Grass grub		larvae	starlings and gulls	8	McLennan & Pottinger 1976
Southern pine beetle			downy woodpecker	5–50	Moore 1972
Southern pine beetle			woodpeckers - summer/winter	12–30, 36–63	Kroll & Fleet 1979
Spruce beetle			woodpeckers - 3 species	45–98	Knight 1958
Spruce beetle	endemic	larvae, beetles	woodpecker	20–29	Koplin & Baldwin 1970
Spruce beetle		larvae, beetles	N. 3-toed and hairy woodpecker	52–83	Shook & Baldwin 1970
Spruce beetle		larvae, beetles	N. 3-toed and downy woodpecker	19–55	Koplin 1972
Spruce beetle	epidemic	larvae, beetles	woodpeckers	24–98	McCambridge & Knight 1972
Western pine beetle			woodpeckers	32	Otvos 1965
Western pine beetle			all but woodpeckers	8–26	Otvos 1970

Table 1. Avian predation on destructive insects.

Insect	Density	Stage	Avian predator(s)	% Mortality	Study
Pine weevil		larvae, pupae	woodpeckers	≤90	Voute 1951
Weevil		larvae, pupae	woodpeckers	95	Voute 1951
OTHER					
Sycamore aphid	endemic	adults	house sparrows	25–69	Dixon 1976
Eucosmid moth		winter larvae	blue & coal tits	50	Gibb 1966
Jumping plant louse		nymphs, adults		≤77	Clark 1964
Fox-colored sawfly			tits, goldcrest	3	Gibb 1960
Fox-colored sawfly				4	Tinbergen 1949
Pine sawfly	endemic	winter cocoons		95	Coppel & Sloan 1971
Sawfly			tits, goldcrest	18	Gibb 1960
Sawfly				24	Tinbergen 1949
Ticks			redbilled oxpecker	95.7	Bezuidenhout & Statterheim 1980

ius and managed with nest boxes did not reach epidemic levels while nearby areas required treatment with insecticide.

Birds have been known to eliminate a destructive insect population in localized outbreak areas. Several cases of localized control have been reported in Europe (Shevrynev 1892, Averin and Shevehenko 1941, Bublik 1954, Bruns 1960, Luhl and Watzek 1976). In North American literature, early work by McAtee (1927) documented the destruction of forest tent caterpillars (*Malacosoma disstria*) by 36 species of birds. Control was also obtained in a 243-hectare (600-acre) outbreak of jack-pine budworm (*Choristoneura pinus*) by several species (Mattson et al. 1968), and by robins (*Turdus migratorius*) on Indian wax scales (*Ceroplastis ceriferus*) infesting holly (Davidson 1975).

Feasibility of Biological Control

There are 1,425 species of pest insects in the United States and Canada. Successful biological control has been reported for 70 of these species. Huffaker et al. (1971) stated that this record is remarkable considering the low level of support biological control research receives in North America. The benefits of a successful biological control program can be enormous. In one documented case, introduction of parasites of the coconut scale (*Aspidiotus destructor*) on the Island of Principe resulted in savings of $2 million over a 10-year period (Huffaker et al. 1971). This represented a 200-fold return in 10 years, after an initial investment of $10,000.

The economic value of bird predation on destructive insects of forest and agricultural lands in the United States was assessed as early as 1921 by Forbush. He concluded that birds reduced insect damage by 28 percent at that time, a savings of $444 million in crop and timber losses.

The value of effective biological control may be considerable over a long time period. Pesticides, on the other hand, may bring about temporary population reductions but do not regulate insect outbreaks. The use of insecticides may prolong outbreaks and/or shorten the time between outbreaks (Holling et al. 1979, Blais 1974). Management with pesticides may require repeated insecticide applications.

Western spruce budworm have been a problem in the Pacific Northwest since the 1940s. Budworm defoliate economically valuable Douglas-fir (*Pseudotsuga menziesii*), true firs (*Abies* spp.), and spruce (*Picea* spp.). In Oregon and Washington, 5.5 million acres (2.2 million ha) were sprayed to control the budworm between 1949–1979 at a cost of $9 million (Dolph 1980). DDT was sprayed on 4.7 million acres (1.9 million ha) between 1949–1962 at a cost of approximately one dollar per acre. Recent control programs utilizing short-lived insecticides have become much more costly. The last widescale project in Washington cost $7.77 per acre (Dolph 1980).

The most effective insecticide used on the budworm (Sevin-4-Oil) decreases larval densities by 80 percent when other mortality factors are not considered (Mounts et al. 1978). In comparison, avian predators of western spruce budworm cause 72 percent of the mortality on larvae and pupae (Campbell and Torgerson 1982). Based on a cost-benefit analysis of the northern Washington area (USFS 1977a), the effect that avian predators have on the budworm is worth a minimum of $3770 per square mile in an outbreak year (Takekawa and Garton 1982). This figure does not include the potential benefits birds contribute in preventing insect outbreaks, a value which may be extremely high.

Managing Avian Predators

The Europeans have used birds to control destructive forest insects for hundreds of years (Henderson 1927, Otvos 1979). Forest birds have been legally protected since the early 1300s (Boesenberg 1970). In North America, there are 640 species of breeding birds. Of these species, 283 forage in forested areas and consume insects in 10 percent or more of their diet (Jackson 1979). Management of these species is possible through habitat alteration or through provision of specific habitat requirements.

Cutting Practices

Habitat alteration to increase bird densities is possible through silvicultural methods, snag management, and understory treatment. Cutting practices such as thinning or selective logging may be chosen to increase avian predation on defoliators by maximizing the biomass of predators relative to the volume of foliage available for the insect. Franzreb and Omhart (1978) found that selection harvesting in Arizona that did not change foliage height diversity resulted in an increase in the number of birds per unit of foliage.

Thomas (1979) presented the habitat preferences of birds in the Pacific Northwest in a format that qualitatively relates the effect of forest manipulations on bird populations. In upland spruce-fir stands, Crawford and Titterington (1979) observed bird populations along a continuum of several treatments. They concluded that bird densities were dependent upon the mix of hardwoods and softwoods, and vertical and horizontal structure of the stand, and the level of insect outbreak.

Webb et al. (1977) determined which bird species were affected by different cutting practices in hardwood forests. Garton et al. (1981) are determining how silvicultural treatments change the abundance of avian predators on western spruce budworm.

These papers and others suggest that cutting guidelines could be implemented to encourage avian predators of destructive forest insects, especially in areas where insects are a chronic problem. The most economically feasible way to manage for avian predators is based on a favorable cost-benefit analysis. The expense of applying a certain cutting practice should be offset by the benefit derived from additional avian predation.

Snag Management

The benefit of leaving snags for cavity nesting birds has been well-documented (Thomas et al. 1975, McClelland and Frissell 1975, Scott et al. 1977, Scott 1979, McClelland 1979). In North America, 85 species use cavities, and the majority of these birds are insectivorous (Scott et al. 1977). Forest Service snag policy recognizes the value of leaving snags for birds and recommends that snags and other forest components beneficial to wildlife should be retained (USFS 1977b).

Woodpeckers (Picidae) are primary snag users and are known to contribute significantly to the mortality of Coleopteran adults and larvae (Knight 1958, Otvos

1965, 1970, Koplin and Baldwin 1970, Shook and Baldwin 1970, Koplin 1972, McCambridge and Knight 1972, Moore 1972, Kroll and Fleet 1979). Snag management is essential to maintain populations of these valuable predators since they do not seem to respond to nest boxes.

Undergrowth Management

Habitat conditions for desired bird species may be enhanced by altering the understory of a forest. Kilgore (1971) reported that clearing and prescribed burning of understory brush and saplings in Sequoia forests changed the species composition of the bird community but not total biomass. Bock and Lynch (1970) found greater numbers of species on burned plots when compared to unburned plots. Brush-ground feeders and granivorous species were more abundant in burned areas, while foliage-searching birds predominated in unburned areas.

Our observations in Pacific Northwest forests over the past three years suggest that the understory layer may be one of the most important components determining avian predator numbers. Most birds select patchy habitats with well-developed shrub layers (DeLoach 1970, Thomas et al 1978). The importance of stand structure on predator effectiveness was demonstrated for woodpeckers (Shook and Baldwin 1970). Woodpecker predation on spruce beetle (*Dedroctonus engelmannii*) ranged from 71 percent in open areas to 83 percent in semi-open areas, and to 52 percent in densely stocked areas where insect densities were the same.

These studies suggest that understory management in insect-damaged areas should maintain a semi-open canopy where openings are interspersed to promote a good shrub layer. Our research on avian predators of the budworm seems to support this contention.

Nestboxes

Outside of a few research plots (Dahlsten and Herman 1965, Dahlsten and Copper 1979), there are few cases in North America where manipulations have been used to encourage avian predators of insects. Manipulations are widely used to increase bird densities in European forests (Henderson 1927, von Haartman 1956, Bruns 1960, Franz 1961, Campbell 1968, McFarlane 1976, Otvos 1979). The most commonly used management practice is to erect nest boxes to attract insectivorous holenesting species. Thomas et al. (1975) reported that 400,000 nest boxes are in use in western European forests and 300,000 are established in Spain where management favors *Parus*, *Certhia*, and *Sitta* species (Ceballos 1968).

Pfeifer (1963) reported 6- and 25-fold increases in numbers of adult birds on sites where nest boxes, nest pockets, bundles, and branch piles were added. A 22-year study conducted in Czechoslovakia (Tichy 1967) tested several nesting treatments in a pine stand with poor site conditions. Two experimental stands were censused initially from 1955 through 1957. In 1957, nest boxes were supplied at densities of 5 and 7 boxes per hectare. Bird densities increased 4 and 5 times in the first year of management. In subsequent years, other techniques were applied, resulting in a 19-fold increase from 1955–1966. One surprising aspect of the study was an increase in species diversity. Nestboxes increased diversity 2.5 times while the other manipulations caused a 5-fold increase. By 1966, the number of species had increased 8 times above the initial level.

A study in Russia by Pyl'tisina (1956) showed that when nest boxes were provided, Lepidopteran larval densities decreased 9.5 and 4 times, far greater than adjacent control plots, which declined 4 and 2.5 times. On plots with *Ocneria dispar* and *Tortrix viridana* outbreaks, densities of 4 nestboxes per hectare resulted in avian control of 47.3 percent. Where 10 nests were supplied per hectare, birds accounted for 80.2 percent and strongly contributed to control the outbreak. Further studies on *T. viridana* indicated that avian-caused mortality increased from 1.9 percent without nest boxes to 54 percent with 10 boxes per hectare, 98.1 percent with 15 boxes per hectare, and 99.2 percent mortality with 20 artificial nests per hectare.

Strokov (1956) found that 12–18 nests per hectare was the most efficient nest density to use when the habitat was poor. At higher bird densities, it was possible to use only 5 nests per hectare to achieve the same result. They also found that gourds could be used effectively as artificial nests in place of wood or concrete-and-sawdust boxes at one-third the cost.

Other Methods

Our studies on avian predators of the western spruce budworm in the Pacific Northwest have identified flocking species such as the evening grosbeak (*Hesperiphona vespertina*), pine siskin (*Pinus spinus*), and red crossbill (*Loxia curvirostra*) as the most important avian predators at low epidemic levels. The 283 insectivorous species in North America are 70 percent migrant and 30 percent resident, and only 23 percent nest in cavities while 42 percent nest on the ground. Sixty-seven percent of these birds forage on shrubs, 55 percent forage on trees, and 28 percent are flycatchers. This suggests that other avian species beside holenesters may be important biological control agents in North American forests.

Studies in Russia and Czechoslovakia have shown that other manipulations may be effective in increasing the densities of forest birds. Ground-nesting birds were studied in Russian forests by Titaeva (1956). Thorough investigations were made of 170 nests, identifying variables associated with the nesting area, the microsite, and the nesting spots. He found that certain microsites on the ground were used repeatedly by the same types of birds, and shrub-nesting species selected the same type of tree or bush. Nest sites were created by trimming bushes to create branch clusters and by setting out artificial bifurcations of 2–3 bound branches. Nest platforms were also provided for *Turdus* spp. The greatest success resulted from trimming thickets to create nest sites in areas where the thickets were interspersed with open glades. A similar study by Tichy (1967) showed that adding pine pockets and bundles, managing undergrowth, binding brush thickets, and supplementing winter foods resulted in 4- and 5-fold increases in species inhabiting a pine woods.

Transplant studies have shown that birds can be transferred to areas of insect infestations with good results. Different techniques that have been tried include releasing adults (Treus and Uspenskii 1956), releasing nestlings (Schcerbakov 1956), and releasing nestlings with adults at a ratio of 10:2 (Polivarov 1956). These researchers concluded that transporting adult birds early in the breeding season to areas managed with nest boxes resulted in the best holenester increases (Poznanin 1956).

Other potential methods to enhance birds are feasible. Williams and Koenig

(1980) studied the water dependence of birds and suggested that the local distribution of some species may be limited by the availability of water. Water was especially important for birds inhabiting mesic areas where seasonal droughts occurred. Open water sources were used by 24 of 45 species and almost all granivorous bird species used them frequently. Granivorous species made up the majority of the avian predators that we studied consuming budworm. Their water dependence may allow management of their densities by supplying water sources.

During our first two field seasons (1979–80), we noticed a 10-fold increase in birds misnetted near a log that had been salted to attract game animals. Bird species depend on the availability of trace elements in their diet and sodium may be limiting in some cases. Studies by Lawrence (1980) and Dennis (1975) on birds attracted to feeders point out that many granivorous birds are highly attracted by crystalline salt. Supplying salt for birds may be one means of attracting flocking birds to potential outbreak areas.

Discussion

European forest managers have long used manipulations and management practices to increase avian predation on forest insects. Very little effort has been directed at songbird management in North America. The discrepancy between the two continents is puzzling.

European forests are largely in private ownership and are much more intensively managed than are North American forests. This suggests that in Europe, management for birds may simply replace species lost through intensive forest management. However, studies in North America have shown that nest box manipulations can increase bird densities (Dahlsten and Herman 1965, Dahlsten and Copper 1979). Perhaps it is more important to note that most chemical insecticide manufacturers are based in the United States and thus, management with insecticides has been strongly encouraged in this country.

Objective evaluation of biological control management must weigh the benefit of using birds against the costs of increasing avian densities over a long period. Simulation modeling may be used to imitate the growth of stands subject to periodic pest outbreaks. The difference between predicted yields with and without birds could be used to evaluate the economic worth of avian predation.

Recent budworm studies suggest that certain small areas having favorable microclimates may harbor pockets of the budworm. These populations increase to pandemic levels when favorable conditions allow rapid population growth (Wellington 1981, Long 1981). If these centers are responsible for outbreaks, biological control management may be applied very efficiently in small areas to achieve population regulation over extensive regions.

Acknowledgements

We wish to acknowledge the U.S. Forest Service Western Spruce Budworm Program (CANUSA) for funding support and Dr. Winifred B. Kessler for editing the manuscript.

References Cited

Appel, O., and M. Schwartz. 1921. Die bedeutung des vogelschutzes fur den pflanzenschutz. NachcB1. dtsch. Pfl SchDienst, Berl. 1:49–50.

Ashby, J. N., and R. P. Pottinger. 1974. Natural regulation of *Pieris rapae* Linnaeus (Lepidoptera: Pieridae) in Canterbury, New Zealand. N. Z. J. of Agr. Res. 17:229–239.

Averin, V. G., and V. Shevehenko. 1941 . O meropriyatiyakh po obogashcheniyu sveklovichnykh polei poleznoi dikoi plitsei, Kharkov, 1941.

Barber, G.W. 1925. The efficiency of birds in destroying overwintering larvae of the European corn borer in New England. Psyche 32:30–46.

———. 1942. Control of earworms in corn by birds. J. Econ. Entomol. 35:511–513.

Berlepsch, H. 1923. Der gesamte volgelschutz, Neudamm 10. Aufl. 301S.

Betts, M. M. 1955. The food of titmice in oak woodlands. J. Anim. Ecol. 24:282–323.

Bezuidenhout, J. D., and C. J. Stutterheim. 1980. A critical evaluation of the role played by the red-billed oxpecker *Buphagus erythrorhynchus* in the biological control of ticks. Onderstepoort J. of Veterinary Res. 47:51–75.

Black, E. R., F. M. Davis, and C. A. Henderson. 1971. The flicker and the southwestern corn borer in Mississippi. Proc. Tall Timbers Conf. Ecol. 2:285–292.

Blais, J. R. 1974. The policy of keeping trees alive via spray operations may hasten the recurrence of spruce budworm. For. Chron. 50(1):19–21.

———, and G. H. Parks. 1964. Interaction of evening grosbeak (*Hesperiphona vespertina*) and the spruce budworm (*Choristoneura fumiferana* (Clem.)) in a localized budworm outbreak treated with DDT in Quebec. Can. J. Zool. 42:1017–1024.

Bock, C. E., and J. F. Lynch. 1970. Breeding bird populations of burned and unburned conifer forest in the Sierra Nevada. Condor 72:182–189.

Boesenberg, K. 1970. Deutsche akademie der landwirt-schaftswissenschaft (Tagungsberichte) 110:71.

Bruns, H. 1960. The economic importance of birds in the forest. Bird Study 7(4):193–208.

Bublik, G.P. 1954. Ptitsy-druz'ya sada. Sad i Ogorod No. 2.

Buckner, C. H. 1966. The role of vertebrate predators in the biological control of insects. Ann. Rev. Entomol. 11:470–499.

———. 1970. The role of vertebrates in the integrated approach to control. USDA Forest Service Insect and Dis. Lab., Hamden, Conn.

Buckner, C. H., and W. J. Turnock. 1965. Avian predation on the larch sawfly, *Pristiphora erichsonii* (Htg.), *(Hymenoptera: Tenthredinidae)*. Ecology 46:223–236.

Campbell, B. 1968. The Dean nestbox study, 1942–1964. Forestry 41:27–28.

Campbell, R. W., and R. J. Sloan. 1976. Influence of behavioral evolution on gypsy moth pupal survival in sparse populations. Environ. Entomol. 5(6):1211–1217.

———, and T. R. Torgersen. 1982. Compensatory mortality in defoliator population dynamics. Environ. Entomol. (In press).

Ceballos, P. 1968. Proteccion de aves insectivoras. Boletin Servicio Plagas Forestales 115:79–85.

Clark, L. 1964. Predation by birds in relation to the population density of *Cardiaspina albitextura*. Austr. J. Zool. 12:349–361.

Comins, H. N. 1979. The control of adaptable pests. Pages 217–225 *in* G.A. Norton and C. S. Holling, eds. Pest Management, Pergamon Press, N.Y.

Coppel, M., and N. Sloan. 1971. Avian predation, an important adjunct in the suppression of larch casebearer and introduced pine sawfly populations in Wisconsin forests. Proc. Tall Timbers Conf. on Ecol. 2:259–272.

Crawford, H. S., and R. W. Titterington. 1979. Effects of silvicultural practices on bird communities in upland spruce-fir stands. Pages 110–119 *in* Proc. of Symp. Management of Northcentral and Northeastern Forest Nongame Birds. USDA For. Serv., Amherst, Mass. 268 pp.

Dahlsten, D. L., and W. A. Copper 1979. The use of nesting boxes to study the biology of the mountain chickadee (*Parus gambeli*), and its impact on selected forest insects. Pages 217–260 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, eds. The role of insectivorous birds in forest ecosystems. Academic Press, N.Y. 381 pp.

Dahlsten, D. L., and S. G. Herman. 1965. Birds as predators of destructive forest insects. California Agric. (Sept.):8–10.

Davidson, J. A. 1975. A report of Indian wax scale controlled by birds. Proc. Entomol. Soc. Wash. 77(1):165.

DeLoach, C. J. 1970. The effect of habitat diversity on predation. Proc. Tall Timb. Conf. on Ecol. 2:223–242.

Dennis, J. V. 1975. A complete guide to bird feeding. Alfred A. Knopf, N.Y. 286pp.

Dixon, A. F. G. 1976. Timing of egg hatch and viability of the sycamore aphid *Drepanosephrem plantanoides* at bud burst of sycamore *Acer pseudoplatanus*. J. Anim. Ecol. 45(2):593–603.

Dolph, R. E. 1980. Budworm activity in Oregon and Washington 1947–1979. (R6-FIDM-033-1980). USDA Forest Service, Pacific Northwest Region, Portland, Ore. 54pp.

Dowden, P., H. Jaynes, and V. Carolin. 1953. The role of birds in a spruce budworm outbreak in Maine. J. Econ. Entomol. 46:307–312.

East, R., and R. P. Pottinger. 1975. Starling (*Sturnus vulgaris* L.) predation on grass grub (*Costelytra zealandica* (White), Melolonhinae) populations in Canterbury. N.Z. J. of Agr. Res. 18:417–452.

Entwistle, P., P. Adams, and H. Evans. 1977a. Epizootiology of a nuclear polyhedrosis virus in European spruce sawfly (*Gilpinia hercyniae*): The status of birds as dispersal agents of the virus during the larva season. J. Invert. Path. 29:354–360.

——— 1977b. Epizootiology of a nuclear polyhedrosis virus in European spruce sawfly (*Gilpinia hercyniae*): Birds as dispersal agents of the virus during winter. J. Invert. Path. 30(1):15–19

Floyd, E. H., L. Mason, and S. Phillips. 1969. Survival of overwintering southwestern corn borers in corn stalks in Louisiana. J. Econ. Entomol. 62:1016–1019.

Forbush, E. H. 1921. The utility of birds. Bull. No. 9. Mass. Dep. of Agr., Boston. 83pp.

Franz, J. M. 1961. Biological control of pest insects in Europe. Ann. Rev. Entomol. 6:183–200.

Franz, J. M., A. Krieg, and R. Langenbuch. 1955. (n.t.). Viren. Z. Pfl. Ban. 62:724ff.

Franzreb, K. E., and R. D. Omhart. 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80:431–441.

Gage, S. H., C. A. Miller, and L. J. Mook. 1970. The feeding response of some forest birds to the black-headed budworm. Can. J. Zool. 48:359–366.

Garton, E. O., J. Y. Takekawa, and L. A. Langelier. 1981. Impact and management of vertebrate predation on western spruce budworm. Proposal to Canada/U.S. Spruce Budworm Project West. 78pp. (Unpubl.).

George, J. L., and R. T. Mitchell. 1948. Calculations on the extent of spruce budworm control by insectivorous birds. J. Forestry 46:454–455.

Gerasimova, T. O., and V. K. Unterberger. 1956. Experiments on the attraction of insectivorous birds to pine groves and a study of their feeding habits. Pages 49–54 *in* L. P. Poznanin, ed. Ways and means of using birds in combating noxious insects. USDC. Israel program for scientific translations. 138pp.

Gibb, J. A. 1960. Populations of tits and goldcrests and their food supply in pine plantations. Ibis 102:163–208.

——— 1966. Tit predation and the abundance of *Ernarmonia conicolana* (Heyl.) on Weeting Health, Norfolk, 1962–3. J. Anim. Ecol. 35:43f.f.

Glen, D. M., N. F. Milson, and C. W. Wiltshire. 1981. The effect of predation by blue-tits (*Parus caeruleus*) on the sex-ratio of codling moth (*Cydia pomonella*). J. Appl. Ecol. 18:133–140.

Hagen, K. S., R. van den Bosch, and D. L. Dahlsten. 1971. The importance of natually-occurring biological control in the western United States. Pages 253–293 *in* C. B. Huffaker, ed. Biological control. Plenum Press, N.Y. 511pp.

Henderson, J. 1927. The practical value of birds. Macmillan Company, N.Y. 342pp.

Herberg, M. 1960. Drei Jahrzehnte vogelhege zur neiderhaltung waldschadlicher insekten durch die ansiedlung von hohlenbrutern. Archiv fur Forstwesen 9(1):1015–1047.

Herberg, M. 1965. Bird protection for control of injurious insects and its results. Anz-Schadlingk 38pt. 9pp.(Summary in Rev. Appl. Entomol. 55: 495. 1967).

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91:293–320.

Holling, C. S., D. D. Jones, and W. C. Clark. 1979. Ecological policy design: a case study of forest and pest management. Pages 13–90 *in* G. A. Norton and C. S. Holling, eds. Pest management. Pergamon Press, N.Y.

Holmes, R. T., J. C. Schultz, and P. Nothnagle. 1979. Bird predation on forest insects: an exclosure experiment. Science 206:462–463.

Huffaker, C. B., P. S. Messenger, and Paul DeBach. 1971. The natural enemy component in natural control and the theory of biological control. Pages 16–67 *in* C. B. Huffaker, ed. Biological Control. Plenum Press, N.Y. 511pp.

Inozemtsev, A. A. 1976. The dynamics of the trophic links of forest insectivorous birds and their significance in invertebrate population density control. Zh. Obshch. Biol. 37(2):192–204.

———, S. A. Ezhova, S. L. Pereshkol'nik, and C. L. Frenkina. 1980. Evaluation of the total effect of insectivorous birds on invertebrates in an oak-hornbeam forest. Ekologiya 1:65–75.

Jackson, J. A. 1979. Insectivorous birds and North American forest ecosystems. Pages 1–7 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, eds. The role of insectivorous birds in forest ecosystems. Academic Press, N.Y. 381pp.

Kendeigh, S. C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Biol. Bull. Ontario Dep. Lands and Forests, Maple. No. 1.

Keve, A., and G. Reichart. 1960. Die rolle der vogel bei der abrwhr des amerikanischen barenspinners. Falke 7:20–26.

Kilgore, B. M. 1971. Reponses of breeding bird populations to habitat changes in a giant sequoia forest. Amer. Midl. Natur. 85:135–152.

Knight, F. B. 1958. The effects of woodpeckers on populations of the Engelmann spruce beetle. J. Econ. Entomol. 51:603–607.

Koplin, J. 1972. Measuring impact of woodpeckers on spruce beetles. J. Wildl. Manage. 36:308–319.

———, and P. Baldwin. 1970. Woodpecker predation on an endemic population of Engelmann spruce beetles. Amer. Midl. Natur. 83:510–515.

Korol'Kova, G. E. 1956. Studies of the action of insectivorous birds on mass pests in oak forests. Page 55 *in* L. P. Poznanin, ed. Ways and means of using birds in combatting noxious insects. Ministry of Agriculture of USSR, Moscow. 138 pp.

Kroll, J. C., and R. R. Fleet. 1979. Impact of Woodpecker predation on overwintering within-tree populations of the southern pine beetle (*Dendroctonus frontalis*). Pages 269–282 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, insectivorous birds in forest ecosystems. Academic Press, N.Y. 381pp.

Lawrence, L. 1980. To whom the wilderness speaks. McGraw-Hill, Toronto. 180pp.

LeRoux, E. J. 1959. Importance and control of the codling moth, *Carpocapsa pomonella*(L.) (Lepidoptera:Tortricidae), on apple in Quebec. Rep. pomol. Fruit Grow. Soc. Quebec 1959:45–60.

Long, G. 1981. Dispersal. Presentation at the Western Spurce Budworm Conference, 1981. Portland, Ore.

Luhl, V. R., and G. Watzek. 1976. Die wirkung von hohlenbrutenden kleinvogeln auf kunstlich ausgebrachte schadlicher forst insekten. Allgemeine Forst und Jagdzeitung 147(6–7):113–115.

MacLellan, C. R., and A. W. MacPhee. 1971. Cases of naturally-occurring biological control in Canada. Pages 312–328 *in* C. B. Huffaker, ed. Biological control. Plenum Press, N.Y. 511pp.

Mailloux, M., and E. J. LeRoux. 1960. Further observations on the life-history and habits of the codling moth (*Carpocapsa pommonella* (L.) Lepidoptera:Tortricidae), in apple orchards of southwestern Quebec. Rep. pomol. Fruit Grow. Soc. Quebec 1960:45–56.

Mattson, W. J., F. B. Knight, D. C. Allen, and J. L. Foltz. 1968. Vertebrate predation on the jack-pine budworm in Michigan. J. Econ. Enomol. 61:229–234.

McAtee, W. 1927. The relation of birds to woodlots in New York State. Roosevelt Wildl. Bull. 4:7–152.

McCambridge, W., and F. Knight. 1972. Factors affecting spruce, beetles during a small outbreak. Ecology 53:830–839.

McClelland, B. R. 1979. The pileated woodpecker in forests of the northern Rocky Mountains. Pages 283–299 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, eds. The role of insectivorous birds in forest ecosystems. Academic Press, N.Y. 381pp.

———, and S. S. Frissell. 1975. Identifying forest snags useful for nesting birds. J. For. 73:414–417.

Miller, C. A., and I. W. Varty. 1975. Biological methods of spruce budworm control. For. Chron. 51(4):150–152.

McFarlane, R. W. 1976. Birds as agents of biological control. The Biologist 58(1):123–140.

McLennan, J. A. and R. P. Pottinger. 1976. Mortality of grass grub *Costelytra zealandica* and earthworms Lumbricidae during autumn cultivation. N. Z. J. Agric. Res. 19(2):257–263.

Moore, G. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. Environ. Entomol. 1:58–65.

Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39:487–494.

Morse, D. H. 1978. Populations of bay-breasted and Cape May warblers during an outbreak of the spruce budworm. Wilson Bull. 90(3):404–413.

Mounts, J., R. E. Dolph, D. McComb, and T. F. Gregg. 1978. 1977 Western Spruce Budworm Control Program. USDA, U.S. Forest Service, Portland, Ore. 33pp.

Otvos, I. 1965. Studies on avian predators of *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae) with special reference to Picidae. Can. Entomol. 97:1184–1199.

———. 1970. Avian predation of the western pine beetle, Pages 119–127 *in* C. R. Stark and D. L. Dahlsten, eds. Studies on the population dynamics of the western pine beetle. Univ. Calif., Div. of Agric. Sciences, Davis.

———. 1979. The effects of insectivorous bird activities in forest ecosystems: an evaluation. Pages 341–374 *in* J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, eds. The role of insectivorous birds in forest ecosystems. Academic Press, N.Y. 381pp.

Pfeifer, S. 1963. Dichte und Dynamik von Brutpopulationen zweier deutscher Waldgebiete 1949–1961. Proc. XIII Int. Ornithol. Congr.: 754–765.

Polivarov; V. M. 1956. An experiment on the mass transfer of the flycatcher (*Muscicapa hypoleuca*) in steppe oak groves. Pages 111–112 *in* P. L. Poznanin ed. Ways and means of using birds in combating noxious insects. USDC, Israel program for scientific translations. 138pp.

Poznanin, L. P., ed. 1956. Ways and means of using birds in combating noxious insects. USDC, Israel program for scientific translations. 138pp.

Pyl'tsina, L. M. 1956. Action of attacted birds on the population of harmful insects. Pages 56–58 *in* L. P. Poznanin, ed. Ways and means of using birds in combating noxious insects. USDC, Israel program for scientific translations. 138pp.

Roer, H. 1957. Tagschmetterlinge als vorzugsnahrung einiger singvogel. J. Orn. Lpz. 98:416–420.

Rudd, R. L. 1964. Pesticides and the living landscape . Univ. of Wisconsin Press, Madison. 320pp.

Schcerbakov, I. D. 1956. Requirements of the flycatcher (*Muscicapa hypoleuca*) and the great titmouse as to nesting areas and artificial nests. Pages 64–73 *in* P. L. Poznanin, ed. Ways and means of using birds in combating noxious insects. USDC, Israel program for scientific translations. 138pp.

Schlichter, L. 1978. Winter predation by black-capped chickadees and downy woodpeckers on inhabitants of the goldenrod ball gall. Can. Field. Natur. 92(1):71–74.

Scott, V. E. 1979. Bird response to snag removal in Ponderosa pine. J. For. 77(1):26–28.

———, K. E. Evans, D. R. Patton, and C. P. Stone. 1977. Cavity-nesting birds of North American forests. Agric. Handbook 511. USDA, Forest Service Washington, D.C. 112pp.

Shevryrev, I. Y. 1892. Nasekomoyadnye ptitsy i oblesenie stepei. Sel'skoe Khozyaistvo i Lesovodstvo.

Shook, R., and P. Baldwin. 1970. Woodpecker predation on bark beetles in Englemann spruce logs as related to stand density. Can. Entomol. 102:1345–1354.

Simmons, G. A. 1968. Interrelationship of the chipping sparrow and the jack pine budworm. MS Thesis. Michigan Tech. Univ. 50 pp.

SECTION FOUR

Habitat Requirements of Avian Predators

Edward O. Garton

The bird species that are known to consume western budworm can be grouped into guilds based on their foraging activities: flocking, conifer gleaning, shrub gleaning, ground foraging, and flycatching. The birds in each guild show many similarities in feeding behavior, diet, nesting requirements, and taxonomy. Ecological characteristics of the bird species occuring in western forests have been summarized for two regions (Thomas 1979, Verner and others 1982). A series of symposia examined the potential for managing many of these in forest communities (__________). The role of the species known to be important in regulating budworm populations and their habitat requirements are summarized by guild in this section.

6.6.4.1 Flocking guild--In spite of their general classification by ornithologists as seed-eaters (Bent 1968), the members of the flocking guild show the highest rates of consumption of budworm larvae and pupae (table 6-2). These species are unique in the forest bird community in that they are not territorial during the breeding season, but forage widely in flocks (Bent 1968). Because of this, their numbers may increase enormously on sites experiencing budworm outbreaks. These species all nest in conifers or deciduous trees (table 6-2); consequently, they breed more commonly in mature and old-growth stands than in early successional stages (table 6-3). Their occurrence in a particular stand is sporadic from year to year and most likely related to insect abundance. The flocks appear to be nomadic during the nonbreeding period, moving from area to area or even region to region in search of seeds of conifers and other trees (Bent 1968). During the late summer and fall, they consume large quantities of berries. Beyond these general statements, little is known about the specific factors influencing the numbers of these species from year to year and stand to stand.

6.6.4.2 Conifer-gleaning guild--Budworm consumption by the large guild of conifer gleaners (table 6-3) ranges from 2 to over 6 budworm larvae and pupae per bird per hour (table 6-2). These species are all strongly territorial, with consequent stability in numbers from year to year in any particular stand. They hunt for insects on the foliage and small branches of conifers during the breeding season and play a major role in maintaining sparse budworm populations during intervals between outbreaks. The species resident in fir and mixed-conifer forests during the winter--such as chickadees and kinglets--probably consume large numbers of hibernating larvae. The species in this guild are most diverse in mature and old-growth forests, and the total number of birds in this guild increases with increasing volume of foliage (MacArthur 1958, Garton and Langelier, in press). The guild is most abundant in stands with a multistoried canopy and an abundance of shrubs (Garton and Langelier, in press). The habitat requirements of many of these species are well studied (Bent 1963b, 1964a, 1964b, 1964c, 1965a, 1965b, 1968). Some, such as the yellow-rumped warbler and the western tanager, are adaptable and occur widely. Others--such as the chickadees--have specific nesting requirements, which may limit where they occur (Thomas 1979).

6.6.4.3 Shrub-gleaning guild--Members of the shrub-gleaning guild feed in shrubs predominantly and conifers secondarily. Mean consumption rates varied from 1.7 to 6.0 budworm per bird per hour (table 6-2). These species nest in or under shrubs and are less abundant where shrubs are reduced (Garton and Langelier, in press).

6.6.4.4 Ground-foraging guild--Members of the ground-foraging guild feed on the ground and in the grasses, forbs, shrubs, and lower foliage of trees. Mean budworm consumption varies from 1 to 15 larvae and pupae per bird per hour (table 6-2). These species are territorial and do not show major increases in abundance associated with budworm outbreaks. They apparently shift their foraging locations from the ground and low vegetation to the lower portion of the canopy during outbreaks and apply additional pressure toward suppression of outbreaks during the period of initial buildup. Several of these species nest in shrubs, and most depend on the low vegetation in some way. Even those species nesting on the ground require low vegetation to cover the nest. Members of this guild occur in all successional stages and are particularly associated with ecotones (table 6-3).

6.6.4.5 Flycatching guild--Only the Hammond's flycatcher in the flycatching guild consumes many budworm larvae and pupae (table 6-2), but the members of this group probably consume many adults. This guild is most abundant in later successional stages (table 6-3) and in diverse stands with an open canopy structure (Bent 1963a).

6.6.4.6 Other guilds--Some of the other groups of birds occupying forest stands, such as the raptors, are unlikely to play a direct role in budworm population dynamics. Such groups as woodpeckers, however, which feed extensively on tree trunks during winter, and swifts and swallows, which consume large numbers of adult lepidopterans in the air, may be valuable budworm predators. Members of other guilds have been observed to feed on moths. The roles of these groups relative to budworm have not been studied.

6.6.5 Other Mortality-Causing Factors

Robert W. Campbell

Casual observations have shown that insectivorous mammals eat both late instars and pupae. No attempt has been made, however, to quantify the effect of this predation. In the East, Morris (1955) noted that most of the large larvae that drop to the understory are eaten by white-footed mice, *Peromyscus leucopus* Rafinesque. As an influence on eastern budworm population dynamics, however, small mammals have essentially no effect (Morris and others 1958a).

The activity of arthropod predators is seldom reported. Brief mention is made of predation by representatives of several groups, such as a clerid beetle and a snake fly (Carolin 1974), a carabid beetle (Sanders and Frankenhuyzen 1979), and mites (Jaynes and Drooz 1952). But most of the interest in arthropod predators of the budworms has been in spiders

Table 6-2--Budworm consumption, foraging-guild membership, and nesting requirements of 26 bird species that are important predators of budworm[1]

Species	Budworm consumption[1]	Foraging guild	Nesting substrate
Evening grosbeak	36.3	Flocking	Conifers or deciduous trees
Red crossbill	18.3	Flocking	Conifers
American robin	15.0	Ground	Shrubs or low in trees
Pine siskin	12.1	Flocking	Conifers or deciduous trees
Cassin's finch	8.3	Ground	Conifers or deciduous trees
Warbling vireo	6.5	Conifer	Conifers or deciduous trees
Black-capped chickadee	6.1	Conifer	Cavities made by other species
Mountain chickadee	6.1	Conifer	Cavities made by other species
Nashville warbler	6.0	Shrub	Ground
Brown-headed cowbird	5.4	Ground	Parasitic--eggs laid in nest of other species
Chipping sparrow	5.3	Ground	Shrubs or low in trees
Dark-eyed junco	5.1	Ground	Ground
Townsend's warbler	5.0	Conifer	Conifers
Townsend's solitaire	4.0	Conifer	Ground
Yellow warbler	3.7	Shrub	Shrubs, especially riparian willows
Solitary vireo	3.5	Conifer	Conifers or deciduous trees
Yellow-rumped warbler	3.4	Conifer	Conifers
Western Tanager	3.1	Conifer	Conifers or deciduous trees
Golden-crowned kinglet	2.9	Conifer	Conifers
Ruby-crowned kinglet	1.9	Conifer	Conifers
MacGillivray's warbler	1.7	Shrub	Shrubs
Swainson's thrush	1.3	Ground	Shrubs or low in trees
Hammond's flycatcher	1.2	Flycatching	Conifers or deciduous trees
Rufous-sided towhee	1.1	Ground	Shrubs
Hermit thrush	1.0	Ground	Ground
Western wood pewee	.1	Flycatching	Conifers or deciduous trees

---

[1] Budworm consumption (mean number of large larvae and pupae consumed per hour per bird) was estimated from stomach contents and digestive-rate studies.

Table 6-3--Successional stages and ecotones of fir and mixed-conifer forests used for breeding (B) and feeding only (F) by 26 important avian predators of budworm (after Thomas 1979)

		Successional stages						Ecotones		
Foraging guild	Species	Grass-forb	Shrub-seedling	Pole-sapling	Young	Mature	Old-growth	Grass-shrub	Shrub-forest	Grass-forest
Flocking	Evening grosbeak	F		F	F	B	B		B	B
	Red crossbill				F	B	B		F	F
	Pine siskin	F	F	B	B	B	B	F	B	B
Conifer	Black-capped chickadee			B	B	B	B	F	B	
	Mountain chickadee			B	B	B	B		B	B
	Warbling vireo		F	B	B	B	B	F	F	
	Solitary vireo			B	B	B	B			
	Townsend's solitaire	B	B	B	B	B	B	B	B	
	Townsend's warbler				F	B	B			
	Yellow-rumped warbler			F	B	B	B	F	F	
	Western tanager		F	F	B	B	B		B	B
	Golden-crowned kinglet		F	F	B	B	B			
	Ruby-crowned kinglet			F	F	B	B	F	F	
Shrub	Nashville warbler		B	F	F				B	
	Yellow warbler		B	B	B	B		F	F	
	MacGillivray's warbler		B	B	B	B			F	
Ground	American robin	F	B	B	B	B	B		B	B
	Cassin's finch	F	F	F	B	B	B	F	B	B
	Brown-headed cowbird	B	B	B	B	B	F			
	Chipping sparrow	F	B	B	B	B	B	B	B	
	Dark-eyed junco	B	B	B	B	B	B		B	B
	Swainson's thrush		B	B	B	B	B		B	
	Hermit thrush			F	F	B	B			
	Rufous-sided towhee		B	B	B	B	B	B	B	
Flycatching	Hammond's flycatcher		F	F	F	B	B		B	
	Western wood pewee		F	F	B	B	B		B	B

LITERATURE CITED - BOOK 1, CHAPTER 6

GARTON

Section 6.6.4

Bent, A. C. Life histories of North American flycatchers, larks, swallows, and their allies. New York: Dover Publishers, Inc.; 1963a. 555 p.

Bent, A. C. Life histories of North American woodwarblers. New York: Dover Publishers, Inc.; 1963b. 367 p. Part 1. 367 p. Part 2.

Bent, A. C. Life histories of North American jays, crows, and titmice. New York: Dover Publishers, Inc.; 1964a. 214 p. Part 1. 280 p. Part 2.

Bent, A. C. Life histories of North American nuthatches, wrens, thrashers, and their allies. New York: Dover Publishers, Inc.; 1964b. 475 p.

Bent, A. C. Life histories of North American thrushes, kinglets, and their allies. New York: Dover Publishers, Inc.; 1964c. 452 p.

Bent, A. C. Life histories of North American blackbirds, orioles, tanagers, and allies. New York: Dover Publishers, Inc.; 1965a. 549 p.

Bent, A. C. Life histories of North American wagtails, shrikes, vireos, and their allies. New York: Dover Publishers, Inc.; 1965b. 411 p.

Bent, A. C. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies, order Passeriformes: family Fringillidae. New York: Dover Publishers, Inc.; 1968. 602 p. Part 1. 646 p. Part 2. 640 p. Part 3.

Garton, E. O.; Langelier, L. A. Effects of stand characteristics on avian predators of western spruce budworm. Transactions of the International Union of Forest Research Organization. [IS JOURNAL TITLE CORRECT?] [In press].

MacArthur, R. H. Population ecology of some warblers of north-eastern coniferous forests. Ecology. 39: 599-619; 1958.

Thomas, J. W., ed. Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. Agric. Handb. WO-553. Washington, DC: U.S. Department of Agriculture, Forest Service; 1979. 512 p.

Verner, ________ ___.; [and others]. 1982. [PROVIDE NAMES OF OTHER AUTHORS AND COMPLETE CITATION].

SECTION FIVE

EFFECTS OF STAND CHARACTERISTICS ON AVIAN PREDATORS OF WESTERN SPRUCE BUDWORM

By
Edward O. Garton and Lisa A. Langelier
Fish and Wildlife Department, University of Idaho
Moscow, Idaho 83843

ABSTRACT

The tree, shrub and ground layer components of forest stands influence the densities of many bird species which feed on western spruce budworm (Choristoneura occidentalis). In the absence of insect outbreaks these stand characteristics largely determine the species composition and abundance of birds in forest ecosystems. The shrub component appears to be closely related to the abundance of many bird species which prey upon western spruce budworm. Stands in early successional stages, having very diverse and abundant bird communities, appear to be highly resistant to outbreaks of this insect. In later successional stages, potential avian predators are less abundant in more densely stocked, even-aged stands lacking a shrub understory. Stand characteristics thus may influence the population dynamics of the western spruce budworm indirectly through the bird component of the predator complex.

INTRODUCTION

The western spruce budworm Choristoneura occidentalis Freeman (Lepidoptera: Tortricidae) occurs widely in coniferous forests throughout western North America. It is the most destructive defoliator of conifers in this region (Fellin and Dewey 1982). Outbreaks of this insect have led to the spraying of millions of hectares of timberland by public agencies and private companies during the last 35 years (Dolph 1980; Fellin and Dewey 1982). The causes of these outbreaks are complex, involving the action of one or more of the factors regulating western spruce budworm populations, such as host and stand conditions, weather, predators and parasites (Fellin and Dewey 1982). Recent studies by Torgerson and Campbell (1982) demonstrated the significant role that bird predators play in controlling western spruce budworm populations at endemic to moderate densities in north-central Washington. In this paper, we examine the effects of stand characteristics on the abundance of avian predators at the same areas in north-central Washington.

METHODS

An outbreak of western spruce budworm in north-central Washington began in 1970 and spread to cover over 1.3 million ha by 1975. Seven-4-Oil and Malathion were applied to 1 million ha of the outbreak in 1976 (USFS 1977). The outbreak had subsided in most areas by 1979 when we began our field work in the Okanagan National Forest. We established rectangular 11.25 ha plots at 4 sites in the Twisp and Methow River drainages (Twisp River, Rattlesnake Creek, Robinson Creek and Bill Smith Place). These plots enclosed 5 ha plots in which life table data for western spruce budworm were gathered by R. C. Beckwith (Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, LaGrande, Oregon). Each plot was gridded with 6 permanent transects 50 m apart.

Plots were censused for birds during the 1979 and 1980 breeding seasons by walking the permanent transect lines on 10 separate days and recording the distance to each bird or group of birds and plotting the location on a map of the site. Two of the sites (Twisp River and Bill Smith Place) were also censused in 1981. Densities of territorial species were estimated by spot mapping (International Bird Census Committee 1970). Densities of non-territorial species were estimated by Emlen's method (Emlen 1977) applied to groups and then multiplied by average group size at the site. Bird species were grouped into foraging guilds for most analyses (Root 1967).

The structure and species composition of the overstory and understory vegetation at each of the 4 study areas were sampled with 24 systematically placed 0.04 ha circular plots. Total height (±1 m), bole height (±0.1 m), dbh (±2.5 cm) crown radius (±0.1 m) and crown shape were recorded for each tree greater than 2.5 cm dbh. Crown volumes were calculated for host and non-host trees from these measurements using a modification of the program HTVOL (Mawson et al. 1976). We sampled the shrubs and conifer regeneration with parallel 30 m line transects centered on each circular plot. The height, intercept, and shape of each shrub or small tree intersecting the line was recorded. Percent ground cover of grasses, forbs, slash, duff, rocks and bare ground were estimated on 5 Daubenmire plots (0.2 m x 0.5 m) placed along the line.

RESULTS

Budworm populations were declining throughout north-central Washington during the period of investigation and 3 of the 4 sites studied followed this trend (R. Beckwith, pers. comm.). The fourth site (Bill Smith Place) maintained a relatively high density (about 30 large larvae per 100 current-year shoots; Torgerson and Campbell 1982) from 1979 to 1980, after which the density declined dramatically. The bird populations of the study areas responded to these changes in budworm populations. To detect differences due to stand characteristics alone, it was necessary to compare the bird populations during low budworm density years. We could do this by comparing the bird communities during the final census year at each site.

The ground foraging, foliage gleaning, flocking and shrub foraging guilds contained the bird species which most frequently had western spruce budworm larvae and pupae in their stomachs. The density of these 4 guilds exceeded 200 adults per 10 ha at Rattlesnake Creek and Twisp River and totaled about 170 adults per 10 ha at the other 2 sites (Table 1). The abundance of the individual guilds also varied between the sites, with ground foraging species most abundant at Rattlesnake Creek, foliage gleaners and shrub foragers most abundant at Twisp River, and flocking species most abundant at Bill Smith Place (Table 1).

All 4 of the sites had highly heterogeneous vegetation reflecting previous logging activity or other disturbance. Rattlesnake Creek and Twisp River had much higher volume of host foliage (Douglas-fir) than the other 2 sites (Table 2). Canopy coverage showed a similar pattern except that Bill Smith Place was much lower than the other 3 sites due to recent selective harvest. This site also differed from the others in its low percent ground cover of duff and large amount of bare ground and slash. The most dramatic difference between these 4 sites was in the amount of shrubs present; Twisp River had 100 times the amount at Bill Smith Place (Table 2). At Bill Smith Place, shrubs were almost non-existent due to heavy grazing and the recent timber harvest. Rattlesnake Creek also had very few shrubs (Table 2). This was most likely due to grazing by sheep and to the shallow, rocky soils present at the site. The remaining 2 sites had abundant shrubs.

The relationship between the vegetation and bird communities at these sites was complex, but some patterns emerged. The total density of the 4 guilds which feed heavily on western spruce budworm was highest on the sites with high overstory crown volume and declined with decreasing crown volume (Fig. 1). The most significant relationships were between shrub volume and abundance of the shrub foraging and foliage gleaning guilds. These 2 guilds are closely related taxonomically and behaviorally and differ in the percentage of time spent feeding in shrubs and trees. Both guilds were more abundant on sites with abundant shrubs. The shrub guild increased arithmetically (Fig. 2) and the foliage gleaning guild increased asymptotically (Fig. 3). However, such relationships must be treated as qualitative and preliminary because of the small sample sizes.

DISCUSSION

The bird communities of conifer forests of the Northwest must have adapted to changes in stand conditions brought about by natural disturbances such as wildfire, extreme winds, and insect outbreaks. It is likely that changes caused by timber harvesting evoke similar adaptive changes. The patterns observed in this study are consistent with the pattern of change in bird communities during succession. In the spruce-fir community of Yellowstone National Park, Taylor and Barmore (1980) found that species diversity and total abundance of birds increased during the initial phase of succession following fire and peaked when shrubs were most abundant and conifers reached 2-3 m in height. Bird abundance then began a slow period of decline to a minimum when the canopy closed completely. At this stage all understory vegetation had been shaded out and there was a heavy layer of slash accumulating from death in the overstocked stand. As the stand began to diversify in structure, species composition and age as seral tree species died out and were replaced by climax species, the bird community again increased in abundance. As succession proceeded to the old growth or climax condition and the understory layer of forbs, grasses, shrubs and young conifers became important again, the bird community reached another peak in abundance and diversity. The Twisp River site was most similar to this final stage in succession while Rattlesnake Creek resembled the earlier stage prior to shrub development. Bill Smith Place and Robinson Creek are not so easily placed along the sere because of their disturbed condition. Bill Smith Place had the open character of later seral stages but completely lacked the shrub component, while Robinson Creek had a horizontally heterogeneous overstory consisting of dense even-aged patches of Douglas-fir interspersed with openings of shrubs.

The potential predation pressure that birds could apply to forest insects such as the western spruce budworm will vary dramatically during the stages of seral development. During the early seral stages, the large number and diversity of birds should be very effective at searching the limited amount of conifer foliage present. The potential for outbreaks in these stands should be lessened. As the stand ages and a dense, even-aged overstory with a large volume of host foliage develops, the shrub component disappears and bird abundance declines, the predation pressure by birds must decrease to a low level. We would expect these stands to have high potential for outbreak. At later seral stages where diversity increases in both overstory and understory levels and where host foliage volume remains high and bird abundance increases, we believe that outbreak potential would decline again.

Bird predation is only one of the factors influencing stand susceptibility to insect outbreaks, but its potential should be considered when silvicultural plans are developed. In particular, even-aged management systems, decreased rotation lengths, increased herbicide applications and single species management may be questioned on these grounds. Short-term gains in tree growth expected from these techniques could be completely eliminated by catastrophic outbreaks by forest pests such as the western spruce budworm.

ACKNOWLEDGEMENTS

This work was funded by the USDA, Forest Service Canada/United States Spruce Budworms Program, Washington, D.C. We thank L. Safranyik and S. Glover for editorial comments.

REFERENCES

Dolph, R. E., Jr. 1980. Budworm activity in Oregon and Washington 1947-1979. U.S. For. Serv. Pacific Northwest Region Publication R6-FIDM-033-1980.

Emlen, J. T. 1977. Estimating breeding season bird densities from transect counts. *Auk* 94:455-468.

Fellin, D. G., and J. E. Dewey. 1982. Western spruce budworm. U.S. For. Serv. For. Insect and Dis. Leaf. 53. Washington, D.C.

International Bird Census Committee. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. *Aud. Field Notes* 24:722-726.

Mawson, J. C., J. W. Thomas, and R. M. DeGraaf. 1976. Program HTVOL--The determination of tree crown volume by layers. U.S. For. Serv. Res. Pap. NE-354. Northeast For. Exp. Sta., Upper Darby, Pennsylvania.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnat-catcher. *Ecol. Monogr.* 37:317-350.

Taylor, D. L., and W. J. Barmore, Jr. 1980. Post fire succession of avifauna in coniferous forests of Yellowstone and Grand Teton National Parks, Wyoming. pp. 130-145. *In* R. M. DeGraaf (ed.), Management of western forests and grasslands for nongame birds. U.S. For. Serv. Gen. Tech. Rep. INT-86. Intermountain For. Range Exp. Sta., Ogden, Utah.

Torgerson, T. R., and R. W. Campbell. 1982. Some effects of avian predators on the western spruce budworm in north central Washington. *Environ. Entomol.* 11:429-431.

U.S.F.S. 1977. 1976 cooperative western spruce budworm control project. U.S. For. Serv. Pacific Northwest Region, Portland, Oregon.

Table 1. Density of adult birds (number per 10 ha) at 4 Douglas fir stands in north-central Washington during 1980 and 1981.

	Study Site (Year)			
Avian Guild	Rattlesnake Creek (1980)	Robinson Creek (1980)	Twisp River (1981)	Bill Smith Place (1981)
Ground foraging	116	61	77	62
Foliage gleaning	70	60	86	41
Flocking	23	9	5	65
Shrub foraging	5	5	35	0
Subtotal	209	172	203	168
Flycatching	60	58	30	16
Timber drilling	0	4	11	13
Total	274	234	244	197

Table 2. Vegetation characteristics of 4 Douglas fir stands in north-central Washington during 1980.

	Study Site			
Characteristic	Rattlesnake Creek	Robinson Creek	Twisp River	Bill Smith Place
Overstory crown volume (m^3/0.1 ha)				
Host	5720	2770	4480	3190
Non-host	1840	1390	305	1560
Total	7560	4160	4785	4750
Shrub crown volume (m^3/0.1 ha)	3.5	22.8	30.6	0.3
Percent cover				
Canopy	52	48	56	33
Forbs	12	8	8	10
Grass	4	5	6	10
Slash	4	6	11	14
Bare ground	6	3	2	14
Rocks	10	6	2	0
Duff	78	82	84	72

FIGURES

Figure 1. The total density of adult birds (number/10 ha) in the ground foraging, foliage gleaning, flocking and shrub foraging guilds as a function of total crown volume (m^3/0.1 ha) of host and non-host trees at 4 sites in north-central Washington.

Figure 2. The density of shrub foraging birds (adults/10 ha) as a function of shrub volume (m^3/0.1 ha).

Figure 3. The density of foliage gleaning birds (adults/10 ha) as a function of shrub volume (m^3/0.1 ha). Shrub volume is plotted on a logarithmic scale.

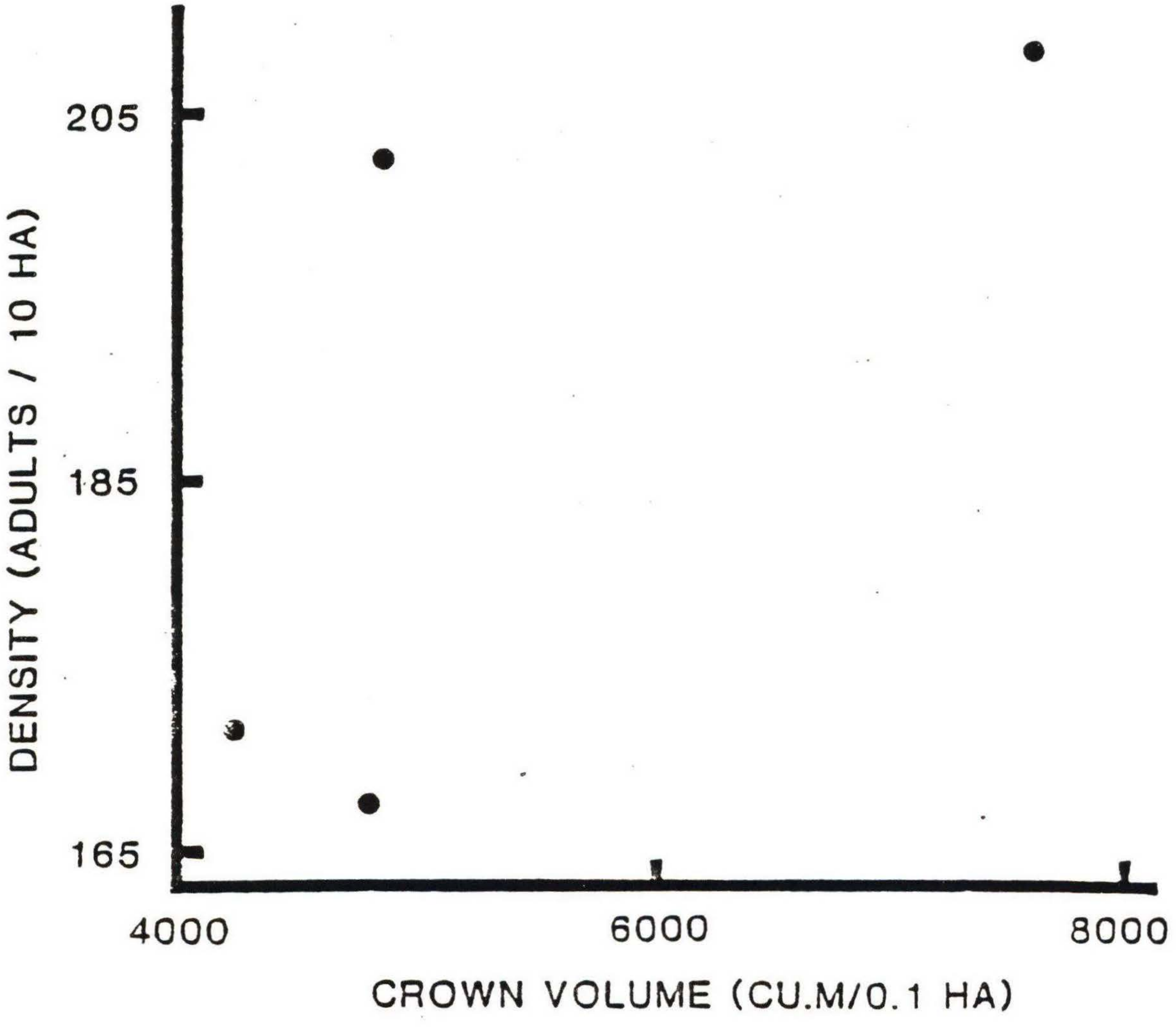

205
185
165
4000
6000
8000
DENSITY (ADULTS / 10 HA)
CROWN VOLUME (CU.M/0.1 HA)

Figure 1.

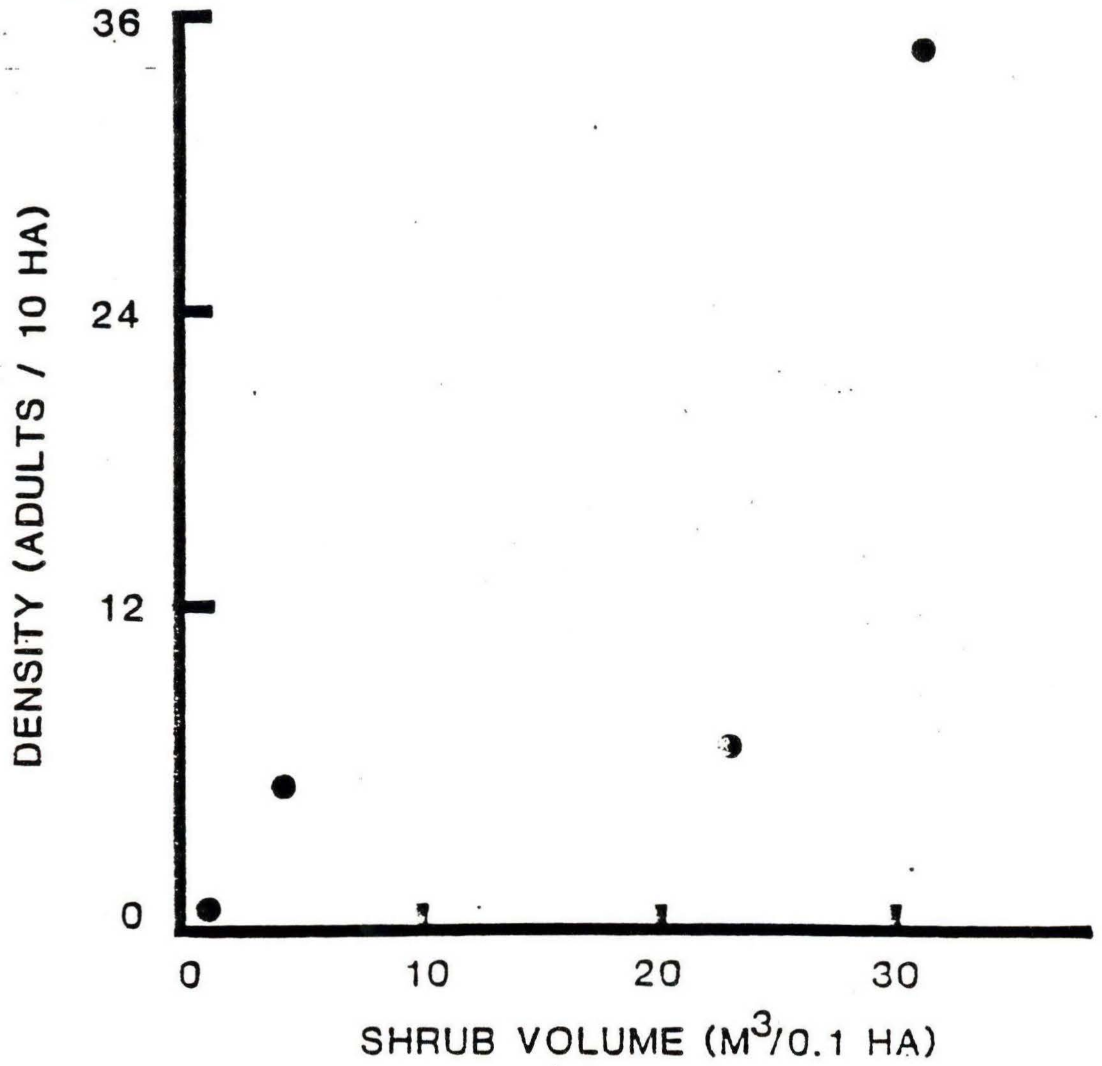


Figure 2.

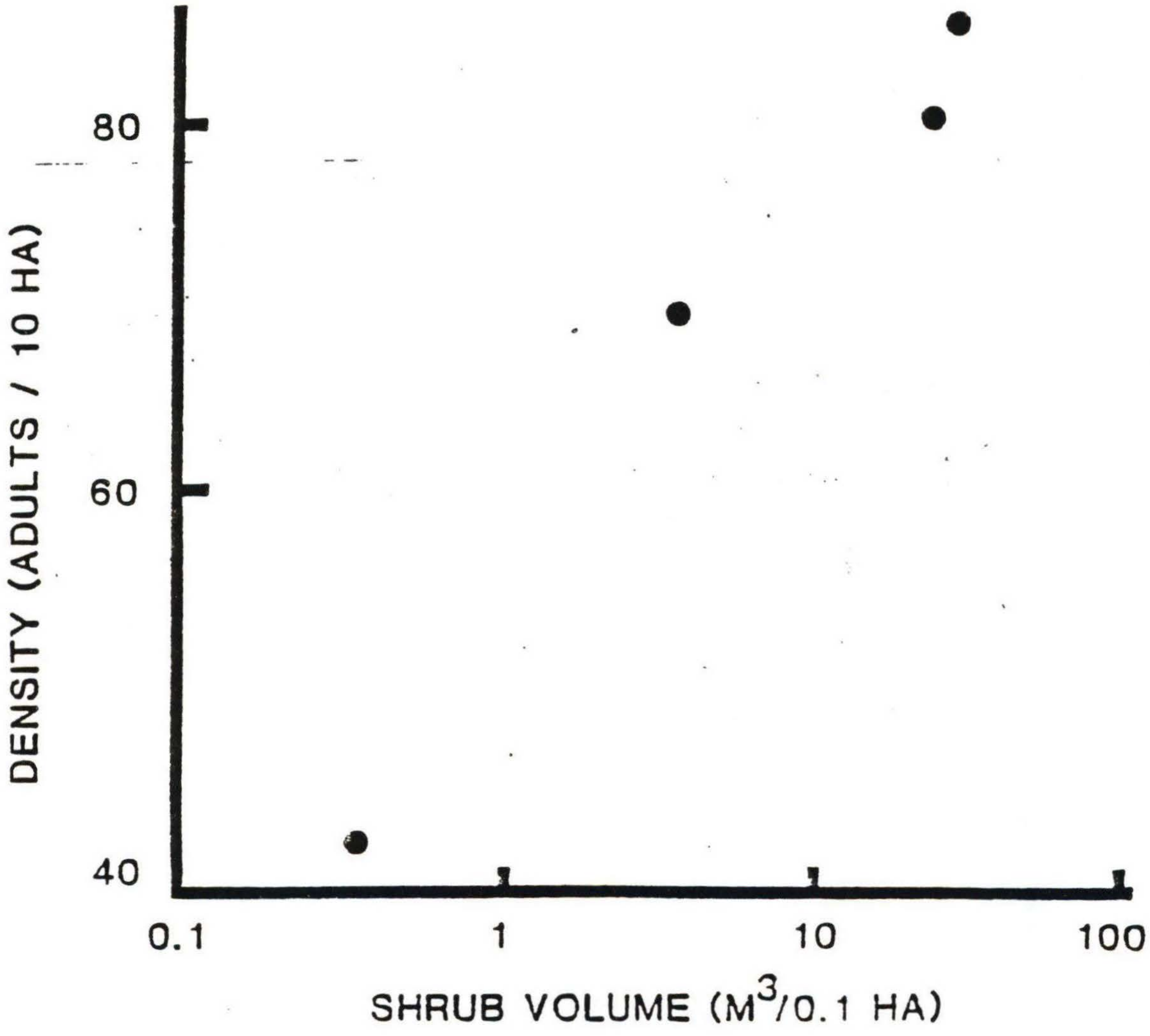


Figure 3.